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# DEVESCOVINID FLAGELLATES OF TERMITES

## I. THE GENUS DEVESCOVINA

BY

HAROLD KIRBY

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# DEVESCOVINID FLAGELLATES OF TERMITES
# I. THE GENUS DEVESCOVINA

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## INTRODUCTION

THE PURPOSE of this monograph is to give a comprehensive account of a group of polymastigotes, the Devescovininae, which is abundantly represented in termites and is rich and diversified taxonomically. Descriptions of a number of devescovinid flagellates have been published, but they are relatively few and many of them are incomplete and inaccurate. I have studied specimens of almost all the species previously described, and accounts of them all are included in the present work.

Members of the subfamily have been found in Mastotermitidae, Hodotermitidae, and Kalotermitidae; but not in Rhinotermitidae, Termitidae, nor in animals other than termites. Present knowledge of their distribution indicates the probability that they will not be found in termites of the last-named two families. There are species in all but six or seven of more than a hundred termites of the genus *Kalotermes* sensu lato which I have examined. As these amount to more than two-fifths of the known species, this monograph may fairly be considered a representative study of existing Devescovininae.

The devescovinid flagellates constitute in their evolutionary aspect a series unsurpassed in any similarly restricted group of Protozoa. Certain species of *Foaina* have the structural elements of trichomonad flagellates in almost their simplest possible form, and at the other extreme are some of the most highly developed polymastigotes. Between the extremes are series which are closely intergraded with respect to elaboration of various organelles of the flagellate body. The biologist who wishes to study the evolutionary history of flagellate or ciliate Protozoa is limited mainly to interpretations derived from consideration of existing forms; and in this group of polymastigotes he should find material for exceptionally productive analysis.

Flagellates of the trichomonad type, to which the Devescovininae belong, are generally of small size. In the Devescovininae, however, there are many relatively very large species, and details of organization are advantageously revealed in them. The axostyle, known in other polymastigotes as a simple fibril or rod, shows an unexpected complexity, sometimes undergoing development far beyond what is apparently necessary to provide for the functional needs of the organism. The parabasal apparatus is elaborated even more; indeed, the tracing of development of that organelle from a condition of extreme simplicity to one of maximum complexity is one of the most significant results of the cytological study of devescovinids. Other characteristics of the flagellates are similarly rewarding to the student of the cytology of Protozoa.

Reproduction by binary fission is the only type known in polymastigote flagellates. When the division process takes place in flagellates in termites, it is likely to occur in a large proportion of a faunule; and there are ways of stimulating division. Consequently, dividing flagellates may be found in large numbers, and thousands of instances of reproduction in Devescovininae have been studied. This fact, together with the large size of many of the flagellates, has facilitated analysis of the trichomonad type of binary fission. Existing knowledge of the process has been supplemented particularly with regard to the origin and fate of organelles in reproduction.

Symbiotic microörganisms are associated extensively with Devescovininae, as with other flagellates of termites. Schizomycetes adherent to the surface by their full length or by one end are of common occurrence, and there are intracytoplasmic microörganisms of many kinds. Particularly with respect to the forms attached to the surface, the study of Devescovininae has contributed significantly to knowledge of the symbionts of Protozoa.

In this paper, after a general account of procedure and of the subfamily, only the genus *Devescovina* is discussed. The position given it does not signify that it is the lowest genus, but there are advantages in using it as an introductory form. Subsequent papers will deal with the other genera; then general accounts will be given of the division process, the parabasal apparatus and other morphological characteristics, host relationships, and distribution. The associated microörganisms must in some degree be dealt with in consideration of the organization and taxonomy of the flagellates, but a comprehensive account must be postponed to a later section.

## ACKNOWLEDGMENTS

In the accumulation, preparation, and illustration of the Devescovininae, together with other flagellates of termites, I have received assistance from many sources, to all of which I make grateful acknowledgment.

Dr. L. R. Cleveland has furthered my work from the beginning. Termites in Panama and Costa Rica were collected with the aid of a grant made to him by the Bache Fund of the National Academy of Sciences. My work in Central America, in which I received assistance from Mr. James Zetek, was done mainly at the Barro Colorado Island Station of the Institute for Research in Tropical America. Cleveland has also sent me for study material from his own collections, particularly many of the flagellates collected for him from termites of Java and Ceylon by Miss Jane Collier, and Devescovininae in a large collection made by himself in New Zealand and Australia. Mr. G. F. Hill and Mr. F. G. Holdaway have sent various termites from Australia, both direct to me and to Cleveland. Dr. S. F. Light has aided me repeatedly in obtaining material, and has turned over to me flagellates from a number of termites of western Mexico collected by him while traveling in the interests of the Termite Investigations Committee. Preparations were made from termites in the Galápagos Archipelago and elsewhere by Dr. A. E. Larsen, on the Templeton Crocker Expedition of the California Academy of Sciences. Termites from Hawaii were sent by Mr. D. T. Fullaway, and preparations of two termites from there were made by Dr. A. M. Adamson. A number of specimens were

obtained in Ecuador by Dr. Wolfgang von Hagen. Dr. G. W. Kidder gave me some slides from a Philippine termite; and Professor E. M. Miller, of the University of Miami, has sent termites from Florida. By the kindness of Professor F. Silvestri it has been possible for me to study specimens of the Devescovininae described by Foà and by Grassi. Professor P. P. Grassé and Colonel Froilano de Mello supplied slides of certain material that they had described.

The studies in Africa, Madagascar, and Java were facilitated by many persons and agencies. I made the trip as a John Simon Guggenheim Memorial Fellow. Through the intercession of the Foundation, the State Department arranged for many courtesies in travel. In Egypt, the Entomological Section of the Ministry of Agriculture provided laboratory space and facilities for collecting trips, on which I was aided by Dr. A. D. Hanna. In Tanganyika Territory, quarters were granted by Mr. W. Nowell, director of the East African Agricultural Research Station at Amani, and courtesies were extended by various members of the staff of that institution. In Nairobi, Dr. V. S. G. Van Someren provided facilities at the Coryndon Memorial Museum. In Kampala, the work was carried on at the Agricultural Laboratories of the government of Uganda. M. Jean van Peborgh, director of the Parc National Albert, arranged opportunities for study in that reserve, though for lack of time full advantage could not be taken of them. In South Africa, Mr. D. Coghill assisted in work near Durban, and, through Mr. R. T. Hall, arranged facilities for travel through a large part of the country. The government of France and the administration of Madagascar furthered the studies carried on in that colonial possession. In large part, the work in Java was only made possible through the extremely generous coöperation of Dr. L. G. E. Kalshoven and the Instituut voor Plantenziekten in arranging for shipment of logs containing termites from various parts of Java and from Sumatra, in providing quarters, and in furthering collecting in the vicinity of Batavia and Buitenzorg. On this expedition to Africa, Madagascar, and Java, and in connection with other aspects of the studies, much aid was given by Margaret Thomson Kirby.

Dr. A. E. Emerson, Dr. S. F. Light, and Dr. T. E. Snyder have contributed to this monograph by determination of the termites. Dr. Emerson has also turned over to me certain material and has checked all the names used for the hosts. The termites designated as new species were, unless otherwise indicated in the text, so distinguished by him.

Grants in aid of the study of Devescovininae have been received from the Research Board of the University of California, the National Research Council, Work Projects Administration, Official Project 165–1–08–73 unit C 1, and Sigma Xi. The grant from Sigma Xi has also made possible the purchase of certain material. Technical assistance has been given by Elmer R. Noble, Mrs. Joy Barnes Cross, and Mr. Jacob Frenkel; and Miss Jane Collier generously gave her services in the staining and sectioning of part of the African collection. Drawings have been made by Miss Dorothy G. Harris; and, more recently, by Miss Agnes Hensley and other personnel supplied by the Work Projects Administration. Many of the illustrations in the later parts of the monograph have been made, with admirable skill and care, by Mr. Carl Stover.

## MATERIAL AND METHODS

Certain methods used in the collection and preparation of material have been described in my earlier papers. In the present account, however, it seems desirable to bring together and extend the account of procedure.

Termites of the genus *Kalotermes* sensu lato, a genus which includes most of the hosts of Devescovininae, and most members of which contain Devescovininae, are obtained from the relatively firm wood of stumps, dead branches, logs, or dead parts of trunks of trees. Infrequently, species are found penetrating living wood. Some species, particularly members of the genus *Cryptotermes,* have been obtained from boxes, furniture, and wood of houses.

In exploring a colony of termites, it is important to secure soldiers and, if possible, winged forms and members of the functioning reproductive caste. These, at least the first, are desirable for identification purposes, and should be preserved intact in alcohol. Only if host specimens are retained can the data gained by study of the Protozoa have their full value in host-parasite correlation studies. Even if determination of the host is possible at the time of capture, permanent preservation of identifiable specimens is generally essential. Such specimens have been obtained in association with all the preparations of Protozoa which I made in Central America, Africa, Madagascar, and Java; and preserved specimens exist of many, though not all, of the hosts obtained in other ways. For the most part, the specimens are in the collection of Dr. A. E. Emerson. In this monograph, as well as in other recent papers, the collection numbers of both the termites and the Protozoa are given. This is necessary, particularly in the absence of determination of many of the hosts, to provide an opportunity for later completion of correlation studies.

Much of the work in Africa and Madagascar was done under conditions of continual travel. Termites found near the road in the course of a one-way automobile trip were collected during the day. Wood and termites were placed in containers; and in the evening, or, if necessary, on subsequent days, observations were made of living flagellates, and preparations were preserved. For the work of preparation, a kit was carried which contained the necessary chemicals and apparatus, so arranged as to be ready for use without delay.

The entire posterior gut was removed from a termite by holding it in the region of the thorax with one pair of forceps and grasping the posterior part of the abdomen with another. If the gut failed to come out intact, or if the abdomen tore off, the material was discarded unless the termites were very few. An attempt to open the tissues often results in fat in the smears, which depreciates the value of the preparation. The gut was placed on a coverglass or slide, the former being much more convenient in field work. The gut was opened, and the contents emptied out with as little mechanical damage to the Protozoa as possible. The flagellates were then gently spread over the substratum. If necessary, a small amount of fluid as nearly isotonic as possible with the contents of the termite gut (0.6 per cent sodium chloride has been much used) can be used for dilution. Too much fluid results in loss of Protozoa in the fixative, and usually dilution is not essential. A good preparation can always be made without dilution; and if dilution is attempted, failure may result.

Smears were made on No. 1 circular coverglasses (thicker coverglasses should not be used under any circumstances) and were fixed and carried through subsequent treatment in "Columbia" coverglass staining jars. Then, separated by paper rings, the coverglasses were stored in alcohol in shell vials. The rings keep open between the coverglasses a space containing alcohol for preservation of the Protozoa, and prevent crushing. It is desirable to put some absorbent cotton in the shell vials, on the bottom and between groups of a dozen or two coverglasses, as this retains in the vial a greater amount of alcohol for preservation of the Protozoa and, later on, facilitates removal of the coverglasses. This method of preserving smears was reported independently by Chen (1937, Parasitology, 23 : 112) for use with opalinids. The shell vials may be placed in groups in jars with cotton and alcohol, or may be stoppered. Thick-walled shell vials are desirable to reduce the hazard of breakage.

In addition to smears, entire guts from many hosts were fixed and preserved in vials; soldiers of the host species may be put in the same vial, for certainty of association with the proper termite. Later, these guts were sectioned. For study of many of the flagellates, though more for some others than for Devescovininae, sections are desirable. If for any reason smears cannot be made, such whole gut material can be used for study of the Protozoa, though with more difficulty and less satisfaction.

Feeding of the termites on moist filter paper may improve the preparations and promote the occurrence of division. For this purpose some termites were removed from wood and, in the course of travel, carried for four or five days in a metal box with filter paper, after which smears were made.

In field work the fixatives used were Schaudinn's fluid, Flemming's fluid, and Hollande's fluid. These have been found sufficient to reveal all structures that I wished to study in Devescovininae. Champy's fluid can be used instead of Flemming's fluid, and has some advantages over it. Bouin's fluid is satisfactory, and if necessary the material can be left in this for a long time. Heidenhain's iron-haematoxylin, Regaud's haematoxylin, and Delafield's haematoxylin are adequate for staining. The last-named stain has been used only for the parabasal body, which, in suitable preparations, it stains intensely after Schaudinn fixation. Counterstaining may occasionally be done, but if preparations of all the other types are available it is unnecessary, and may even hamper observation of details.

In my study of flagellates of termites it has been found that reference to material of the described species, and not to the descriptions alone, is essential. Many of the descriptions are of flagellates of hosts that are in settled regions and can be obtained again without too great difficulty, with certainty of finding the same Protozoa. Of many others, however, that is not true; and sometimes, because the host was not determined, it is almost impossible to know what a writer actually studied. Slides of the original material have seldom been found available. My work has been greatly facilitated by the fact that, although efforts to find Grassi's original material were unsuccessful, Professor Silvestri had a few smears which he had retained from the termites supplied to Grassi. Type specimens ought to be preserved and properly filed, as indeed should be obvious; but it is apparently not the usual practice among protozoölogists. It is not sufficient simply to have the boxes of slides somewhere in one's laboratory, where the specimens might be found after more or less prolonged search of the collection and records. With a large number of termite species represented, many of which are undetermined, it has been necessary to develop a more systematic method.

In the hope of doing this, certain slides bearing each new species have been designated as "syntype" slides. Usually, in the following monograph, there are listed under a species several slides, all derived from the same colony of termites and bearing the same faunules. The record numbers of these slides, designated by TP-, are listed in the publication, to avoid any possible later confusion. Preparations selected from the same host species of termite, but not necessarily the same colony, as the syntype, are designated "xenosyntype" slides. Slides from other termite species bearing the same flagellate species, as ascertained by comparison with preparations from the type host, are denominated "homosyntype" slides. The filing of such slides, and publication of their numbers, should eliminate confusion with respect to occurrence of the species. If at any time a change in determination is necessary, it can be made readily with exact reference to the earlier publication. The host from which the material came also has a number, designated by T-. In the absence of preserved specimens of the insects, T- numbers have sometimes been given to termites to correspond to the slides. These numbers relate, however, to records, and in some degree fix the host. In the following account there appears also, in parentheses, in connection with T- numbers, the name of the person who had the termite in hand and determined it—or had it determined, if that was done.

For filing the selected slides, "Brown Micro Slide Holders," supplied by Arthur H. Thomas, Philadelphia, have been used. These aluminum holders, receiving four slides each, have been described by J. H. Brown (Science, 65:501, 1927). They are filed in standard 3 by 5-inch library-card trays, and the species are referred to on guide cards. Records and cross references can be made on bibliography cards along with each group of slides. I am aware of no method of filing slides which, for the type material of these flagellates, approaches this in convenience and efficiency.

## DESCRIPTIVE AND SYSTEMATIC ACCOUNT

### Subfamily DEVESCOVININAE Kirby

**Devescovinidae Poche, 1913, Arch. Protistenk., 30:153.**

**Devescovininae Kirby, 1931, Univ. Calif. Publ. Zoöl., 36:215.**

***Type genus.*—*Devescovina* Foà.**

***Diagnosis.*—Flagella arising in a single group of several anterior flagella (three in known forms) and one trailing flagellum, which is usually stouter and longer than the others; cresta near base of trailing flagellum a flattened, more or less elongated, subtriangular structure which becomes a large internal membrane in some species; trailing flagellum insecurely adherent to body surface along edge of cresta, but no undulating membrane present; axo-**

**style present, usually well developed; parabasal body present, originally a single organelle which in some respects has branches or appendages; single nucleus, anteriorly situated; flagellates in termites, generally xylophagous.**

## CLASSIFICATION

Poche (1913) proposed the family Devescovinidae to include the one genus *Devescovina.* Doflein (1911) had first used this family name, but without description or assignment of included genera. He listed *Devescovina striata* Foà, 1905, and *Devescovina striata* var. *hawaiensis* Janicki, 1911; and presumably he meant to include only them in the family. In the fourth edition of the textbook (1916) Doflein placed *Devescovina* along with a heterogeneous group of other flagellates with from four to six flagella into the family Tetramitidae Bütschli. In the fifth edition (1927–29) Reichenow followed essentially the same arrangement so far as trichomonad flagellates were concerned. Wenyon (1926) placed various genera of endozoic flagellates characterized by, among other things, the possession of an axostyle and usually a parabasal body, into the family Trichomonadidae, thus separating them from free-living flagellates of the genus *Tetramitus* and other genera. He included *Devescovina, Janickiella,* and *Foaina* in this family. I listed (1931*a*) the subfamily Devescovininae as a subdivision of the family Trichomonadidae.

The second edition of Calkins' Biology of the Protozoa (1933) gives the families Tetramitidae, Trichomonadidae, and Devescovinidae, and includes in the last not only the *Devescovina*-like flagellates of termites, but also *Retortamonas, Tricercomonas,* and *Tricercomitus.* According to the key, the distinction between the Trichomonadidae and the Devescovinidae is the presence in the former of an undulating membrane.

Kudo (1939) placed the endozoic flagellates of the groups with which we are here concerned in two families, the Polymastigidae and Trichomonadidae, according as an undulating membrane was present or absent, both groups having axial structures. But his assignment of genera is in some degree arbitrary: the former family includes *Dinenympha;* and *Tricercomitus,* which has no more of an undulating membrane than does that genus, is put into the latter family.

No arrangement that has yet been made seems entirely satisfactory; here I attempt no more than the designation of Devescovininae as a unified subfamily group, leaving open the question of the position of that subfamily. The relationship of devescovinids to some other flagellates seems too close for the establishment for them, in a balanced system of classification, of the higher family category.

Twelve genera have been described which have characteristics of the Devescovininae: *Devescovina* Foà, 1905; *Parajoenia* Janicki, 1911; *Foaina* Janicki, 1915; *Macrotrichomonas* Grassi, 1917; *Caduceia* França, 1918; *Janickiella* Duboscq and Grassé, 1923; *Paradevescovina* Kirby, 1926; *Metadevescovina* Light, 1926; *Pseudodevescovina* Sutherland, 1933; *Crucinympha* Kirby, 1938; and *Bullanympha* Kirby, 1938. *Gigantomonas* Dogiel, 1916, must be separated from the subfamily, although it resembles devescovinid flagellates in many ways. Since in the original descriptions of some of these genera there are errors and omissions which preclude correct systematic treatment, it is only after reëxamination of the material that one could successfully undertake to clear up matters of generic distinction and synonymy. I have been able to study specimens from the host termite containing the genotypic species of all except *Caduceia,* and have studied in other termites flagellates which belong to the original species of that genus.

A revision of the systematic characteristics must be made, since in many described genera the structures were misunderstood. *Devescovina* is well known, but its characteristics have not been defined sharply enough to prevent inclusion of different devescovinids. *Parajoenia* was erroneously diagnosed by Janicki as having a large number of anterior flagella, and *Foaina* as having two parabasal bodies. *Caduceia* was incorrectly described by França as possessing a complete coat of cilia, and he did not describe the flagella correctly. Light was mistaken, in his diagnosis of *Metadevescovina,* in his description of the tertiary flagella. I did not rightly understand the parabasal apparatus of *Paradevescovina.* Sutherland was wrong about almost all the characteristics she described in *Pseudodevescovina.*

Koidzumi (1921), without having studied either genus, concluded that *Caduceia* is a synonym of *Devescovina,* and in this conclusion Duboscq and Grassé (1927) concurred. These genera were later regarded by Grassé (1937, 1938) as distinct and are so recognized by me (1938*a*). Duboscq and Grassé (1927) thought it probable that *Foaina gracilis* is a predivision stage in the life cycle of *Devescovina hawaiensis,* since they observed "young stages" of "*Devescovina*" *hilli* with a similar double parabasal apparatus, supposedly duplicated prior to division. Grassé (1938) believed it probable that *Foaina* is a synonym of *Parajoenia.* I (1938*b*) found *Foaina gracilis* in *Neotermes connexus.* It has a single V-formed parabasal body; and the so-called young stages of *D. hilli* have also a single parabasal of similar shape, not two. Both clearly belong to the same genus, *Foaina,* but are quite different from *Devescovina.* The relationship to *Parajoenia* is closer, and will be discussed in a later paper. *Foaina* has no characteristics to distinguish it from *Janickiella,* when the various intergrading species described in this paper are considered. *Janickiella* becomes a synonym of *Foaina,* as does also *Paradevescovina.* Grassi (1917), in a postscript to the paper in which he described *Macrotrichomonas,* stated his belief that it is a synonym of *Gigantomonas.* Connell (1932) accepted this conclusion; but after studying *Gigantomonas herculea* I do not agree with it. It is evident that there is much confusion in the classification of Devescovininae, and that the presentation of a monographic account is much needed.

## COMPARATIVE MORPHOLOGY

The flagellates of the subfamily Devescovininae have a considerable range of size, from the small *Foaina grassii,* with a length of 6–16μ, to the large *Pseudodevescovina nova* of 64–114μ (exceptionally reaching 138μ). The range is, however, not so great as in the Trichomonadinae, the smallest of which in termites (*Trichomonas lighti* from *Amitermes*) has a length of 4.5–8μ, whereas the largest (*Pseudotrypanosoma giganteum*) reaches 145–205$\mu$. The tendency to giantism is illustrated both within certain genera and in all members of other genera. In *Trichomonas* giantism is shown, so far as is known, only in the two species *T. termitis* and *T. termopsidis,* which in this respect are separated by a rather wide gap from all other species. Yet the second of these species, with a length of 9 to 85$\mu$, has a range greater than that found in the genus *Foaina.*

The number of specimens measured was large. Where possible, fifty specimens were taken from several slides; in some species a hundred or more were measured. Sometimes data on size were obtained for a devescovinid species from several host species. The results have some bearing on the significance of measurements in differentiating species. *Devescovina lemniscata* averaged 35 by 12.5$\mu$ in one host species, 47 by 20$\mu$ in another, and there was in other hosts a series between these extremes. One species of *Foaina* had an average length of 10.5$\mu$ in one host and 19.2$\mu$ in another, whereas the width remained the same; another measured 31 by 12.5$\mu$ in one host, 21.3 by 7.2$\mu$ in another. Still other size differences might be cited. In all these series the morphological characteristics warranted no species distinctions. There remained the possibility of establishing varieties or forms on the basis of size, but the wisdom of doing this seemed questionable. One would have great difficulty, where a species occurred in several or many hosts, in drawing limits for the subspecific taxonomic groupings, and their establishment would serve no valuable purpose in these sexual organisms. *Devescovina lemniscata,* for example, has a size series which cannot be subdivided except in an arbitrary manner.

The general body size of flagellates in termites, as of other Protozoa, is subject to much variation according as conditions of nutrition, reproduction, and perhaps other factors differ. Particularly large-sized specimens of a species which occur in some termites may be absent in others, and as a result the average measurements would be reduced. Also, the value of exceedingly exact measurements is invalidated by the change of form of the body that may take place under natural conditions or as a result of smearing. When these things are considered, it is apparent that there is no advantage to the taxonomist in applying exact statistical methods to the dimensions of such material. Measurements in small fractions of a micron, even though accurate, are of no significance, even for the average or mean, and this is especially true of measurements carried to hundredths or thousandths of a micron.

The shape of the body of Devescovininae is more constant than that of *Trichomonas,* for active contractions and bendings, like those of *T. termopsidis,* for instance, do not occur. There is no well-defined pellicle, so that the outline can readily be altered passively; and the amount of contained wood determines variation in stoutness and contour, especially of the posterior end. In general, some species are pointed posteriorly and others are broadly rounded; but the different forms may occur within a species.

Though the body maintains a constant shape, there is no well-defined, permanent pellicle. This is indicated by the rotation of the anterior part of the body with the internal organelles while the posterior cytoplasm remains stationary, a peculiar behavior, described later (p. 62) as it occurs in *Devescovina lemniscata* and certain other devescovinids, and observed also in *Pseudodevescovina uniflagellata* (Kirby, 1936). There is no observable evidence of any change in the surface, whereas a permanent pellicle would be twisted apart by this activity.

Probably all flagellates of the subfamily Devescovininae possess three long anterior flagella. There is a papilla along the edge of which the basal parts of the anterior flagella adhere (fig. A; pl. 8, fig. 58). There are visible proximally only two, instead of three, roots along the papilla. The roots of the flagella are not embedded in the cytoplasm of the papilla, and are not firmly united to the surface. They are not infrequently torn loose for part of, or all, the distance to the bleoharoplast, but they are adherent in living and most fixed specimens. The papilla is actively mobile, and its movements accompany activity of the whip of anterior flagella. These movements are lateral bendings, and are vigorous at times. The papilla is relatively large in most species of *Devescovina;* in some large forms, as, for example, *Caduceia* and *Pseudodevescovina,* it is relatively small. The position in which it is fixed determines an apparent variation in the form of the anterior end of the body. If it is fixed at the end of the lateral stroke, it may lie against the surface of the body. This explains failure to describe the papilla in some devescovinids. The papilla is an advanced development of a smaller homologous structure that is often present in *Trichomonas* and related genera, though it has not been shown in most species of that genus and is certainly absent in some.

The trailing flagellum is of much value taxonomically. In length it varies from about half or less that of the body to two or three times the body length, being at a relative maximum in the genus *Foaina.* Its width is a valuable specific character. In some species it is a slender filament hardly stouter than an anterior flagellum; at the other extreme it is, in its middle portion, a comparatively broad ribbon (pl. 8, fig. 60); and there are all gradations between. However broad it may be, at the point of attachment to the body it is always a slender filament, and it tapers to a slender posterior end.

In small devescovinids, and in specimens heavily stained, the blepharoplast often appears to be a single large granule. Most investigators who have studied devescovinids have noted, however, that there are several granules at the point of union of the flagella and other organelles. These may be closely aggregated, so that a heavy stain gives the group the appearance of a single body, as is frequent in *Devescovina* and *Foaina;* in most species of *Foaina,* in fact, only one blepharoplast body has been seen. But in certain larger devescovinids, for example, species of *Macrotrichomonas, Caduceia,* and *Pseudodevescovina,* the granules are widely separated and are interconnected by fibrils. They vary in number and arrangement in different species, and in some of the more highly organized forms their characteristics are of systematic value.

The cresta (fig. A) is present in all devescovinids. It differs greatly in size in different species and is one of the features of greatest value taxonomically. Generally it is used for specific distinction, but the markedly unusual character of the cresta of *Macrotrichomonas* is the main distinction of that genus.

Anteriorly the flat cresta is broadened, giving the structure a more or less subtriangular form. Its edges may be designated in accordance with the method used by Grassi (1917) and Connell (1932) as external, anteromedial, and posteromedial. Within the genus *Foaina* it ranges from a small, almost unrecognizable structure 1.5μ long to a rod as long as the body. In *Macrotrichomonas* it is large and platelike, sometimes two-thirds as long as the body, and half as wide at its broadest point. The size of the cresta is unrelated in general to the size of the animal or to that of the trailing flagellum. Its outer edge coincides with the surface of the body, and the trailing flagellum passes along this and seems to be insecurely adherent. This attachment is easily broken; it is usually separate in fixed material. The cresta is related to the costa of *Trichomonas,* but the trailing flagellum does not form a definite undulating membrane over it, and it has a somewhat different fate in division. In *Trichomonas* the old costa is retained and a new one grows out; in devescovinids the cresta is resorbed and two new ones are differentiated. The cresta is capable of independent motility in some species. This motility has been observed in *Macrotrichomonas lighti* (Connell, 1932) and in *Pseudodevescovina uniflagellata* (Kirby, 1936).

Authors have found it convenient to designate dorsal and ventral sides in trichomonad flagellates. This orientation has usually been based on the position of the clear area that has customarily been regarded as a cytostome; thus, at the anterior end of the body, the side with the costa and undulating membrane is dorsal (Wenrich, 1939). I (1931*a*) identified this area, as most authors have done, as a cytostome. But, as will be discussed at greater length later, that interpretation is questionable. Study of the similar structure in devescovinids has made it seem unlikely that it is a cytostome. Thus, designation of the side it occupies as ventral is arbitrary; there is no natural dorsality and ventrality. Light (1926) designated the side on which, in a notch, the flagella of *Metadevescovina debilis* take origin as ventral. He evidently based this opinion on the erroneous belief that this notch corresponded in position to the supposed cytostome of related flagellates; actually, that clear area is on the opposite side. It seems best to adopt for devescovinids the customary orientation of *Trichomonas,* and refer to the side occupied by the cresta, at least in its anterior part, as dorsal. The situation in both *Trichomonas* and devescovinids is often complicated by the fact that the costa or cresta may follow a spiral course.

The axostyle provides generic and specific characteristics of prime importance. There are two parts of the axostyle: trunk and capitulum. In the genera *Devescovina* and *Caduceia* the trunk typically tapers posteriorly to a filament, which often is sinuous and may be recurved, and is enclosed entirely within the cytoplasm. In other genera the trunk is stout to the posterior end of the body, and usually has a sharpened projecting posterior end. This may be an enlarged, spearhead-shaped cusp, the size of which varies within a species; but it is of value in distinguishing species. Around the trunk, anterior to the cusp, a few species have small rings, a spiral filament, or a muff. The trunk of the axostyle has a sheath and a central core, in which some differentiation may be visible in the larger species. But there is no fibrillar structure; Janicki in *Parajoenia grassii,* Lewis in *Metadevescovina polyspira,* and Connell in *Macrotrichomonas lighti* were mistaken in so describing the axostyle.

The capitulum of the axostyle has undergone a remarkable development in some species of Devescovininae. In the simpler forms the expansion of the flattened part alongside the nucleus does not extend beyond the limits of the nucleus. In most species, however, the margins of the capitulum are visible alongside of and anterior to the nucleus. In certain species of *Metadevescovina,* and to a less degree in *Parajoenia* and one species of *Devescovina,* it is still more expanded, ridges arising from it or membranous extensions reaching far beyond the usual limits of a capitulum. Granules of characteristic form are, in some species, associated with the capitulum, apparently adherent to its free surface.

In view of the relatively simple characteristics of the parabasal apparatus of other polymastigote flagellates, the development that takes place in some of the Devescovininae is remarkable. In some species of *Foaina* the parabasal body is small and of as simple a type as is possessed by any flagellate. In other species of *Foaina,* its length is greater, and it is bent at the posterior level of the nucleus, passing along the membrane and toward the periphery of the body. In *Metadevescovina, Devescovina,* and several other genera it is coiled more or less closely around the trunk of the axostyle posterior to the nucleus. In some species the parabasal body has branches or appendages. A tendency to development of these is widespread in the Devescovininae (Kirby, 1937*c*). Generically, whether or not the parabasal is coiled (this is not merely a matter of length), and several different forms of branching are of systematic value. The length of the parabasal is, within limits, variable; but, allowing for this, it also is of value in species designation.

A parabasal thread, which is situated along the inner margin of the parabasal body, is probably present in all devescovinids, although it is more conspicuous in some species than in others. In many species there is no possibility of mistaking it. Often it is stouter in the more posterior portion of the parabasal than near the blepharoplast, and in some species it extends beyond the other substance at the posterior end.

When stained with Delafield's haematoxylin, after Schaudinn's fluid, the main substance of the parabasal often shows a heterogeneous structure. This is especially true in the genera *Metadevescovina* and *Foaina.* Sometimes there are clear vesicles in the stainable matrix, sometimes distinctly delimited granules or blocks (Kirby, 1931*b*). My observations, reported in detail under some of the species studied, are not in agreement with Duboscq and Grassé's assertion that these Delafield-staining elements are the same as the supposed secretory vesicles described by them.

There is more than one type of nucleus in the Devescovininae, as was noted by Janicki in his studies of *Devescovina, Parajoenia,* and *Foaina.* The nucleus of *Devescovina* is ellipsoidal or ovoidal in form, with little if any irregularity of outline, and its long diameter is usually in the direction of the longitudinal axis of the body. The blepharoplast is at or near its anterior end, either in the longitudinal axis or, more usually, near it on one side. Janicki's accurate description of the nucleus of *Devescovina hawaiensis* applies in general to the nucleus of all members of the genus. The nuclear membrane is well defined. The chromatin is gathered into a central chromatin mass in large and small granules, which stain deeply with iron-haematoxylin. At some point on the periphery of the mass there is usually present a nucleolus surrounded by a clear area. Between the chromatin mass and the membrane there is often a clear space, sometimes fairly broad. Janicki believed that this space between the membrane and nuclear contents is the result of shrinkage under the influence of reagents. It does not appear in the nucleus of *Foaina, Metadevescovina,* or *Parajoenia* treated by the same technique and often on the same slides. Therefore, if it is the result of shrinkage, it nevertheless indicates a difference in the tendency of different devescovinid nuclei to undergo this.

The other type of nucleus occurs in *Foaina, Parajoenia, Metadevescovina,* and some other genera. Its larger diameter is frequently in a transverse or oblique direction. Its outline sometimes shows more irregularities than the other type. The nuclear membrane is often less well defined, and there is generally no clear space under it, the chromatic nuclear contents occupying the entire interior. The chromatin is generally distributed in finer granules than in the *Devescovina* type of nucleus. There are one or two peripheral nucleoli. The chromatin material loses the iron-haematoxylin stain much more readily than in *Devescovina,* whereas the nucleolus retains it tenaciously. The nucleus of *Devescovina* may show numerous black granules when, except for the nucleolus, that of *Foaina,* on the same slide, has lost the stain entirely.

These differences in nuclei are of some value for taxonomic distinction. But the two types are not sharply distinct categories, and do not include all nuclei of Devescovininae. Sometimes, characteristics of the two are combined.

In many species the cytoplasm has no distinct zones of ectoplasm and endoplasm, but in some, as in *Pseudodevescovina uniflagellata* and other large species, there is a clearer peripheral layer. Practically all species of Devescovininae are xylophagous, but they differ in the relative amount of wood that is ordinarily present. Often, there are also large granules, usually of heterogeneous structure, probably products of wood digestion. Numerous small granules are present. Intracellular microörganisms of various kinds, including a nuclear parasite, are frequently found. Some microörganisms are generally distributed in the cytoplasm; others are localized (see Kirby, 1941).

Microörganisms of two types adhere to the surface of certain Devescovininae. The type of microörganism provides a valuable aid in recognition of species, for on any one kind of devescovinid there is found the same type, often on all individuals. The microörganisms are also of value in the recognition of certain genera, although they are, of course, not a taxonomic character. All known species of *Devescovina* have long rods adherent by their full length, generally in a more or less longitudinal direction (pl. 7, fig. 52; pl. 8, fig. 54). These have been mistaken for longitudinal striations, but Duboscq and Grassé have pointed out their true nature (see Kirby, 1941). They have not been found on most other devescovinids, except for certain species of

*Caduceia,* and, where they do occur, it is usually not with the constancy shown in *Devescovina.*

On many Devescovininae there are spirochaetes adherent to one or both ends or investing the entire surface (pl. 1, figs. 3, 5). There are several kinds of these, a particular kind being characteristic of particular devescovinids, sometimes a single devescovinid having two types. In some species practically all specimens have these, either on a particular region or all over the body. Like the *Fusiformis*-like rods, they are of value in recognition of species, and consequently they are mentioned in the diagnosis of each species having them, or their absence is reported.

## THE LIFE CYCLE

In attempting to classify Protozoa on the basis of morphological characteristics alone, without the check on the complete life history which might be gained from maintenance in culture started from a single specimen, there is some difficulty. When as many as five devescovinids are described in one host, as in *Neotermes connexus,* and when two or three are recognized in most hosts, a suspicion is aroused that there may have been error in separating different developmental forms of one species. A reader who has not studied the original material may with some reason doubt that the author has given due consideration to transitional forms, and question whether he has not concluded too hastily that different species are represented.

Ever since (1924) they described the development of *Janickiella grassii* as beginning with very small *Trimitus* forms, followed by avicular forms, post-schizogony rosettes, and *Eutrichomastix* and *Trichomonas* stages, Duboscq and Grassé have contended that there are cyclical stages in termite flagellates. At that time they suggested that *Eulophomonas, Joenia, Mesojoenia,* and *Microrhopalodina* may also belong in the cycle. The latter opinion was, however, soon abandoned. Recently (1934) they concluded that the *Trimitus* forms belong to a separate species, *T. divergens,* and the avicular forms to *Opisthomitus avicularis;* but they were not even then willing to exclude all possibility of an ontogenetic relationship between *Trimitus* and other flagellates. It will be shown later in this monograph that the *Eutrichomastix* stage is *Foaina* (=*Janickiella*) *grassii,* and that the *Trichomonas* stage is a second species of *Foaina.* In their first paper (1923) Duboscq and Grassé correctly described these as separate species.

In the other termite faunules, also, that they studied, they found such cycles. In *Reticulitermes lucifugus* they (1925), following Porter and Grassi, regarded *Dinenympha gracilis* as a young stage of *Pyrsonympha vertens;* and *Microjoenia* was considered (1928) to be a young stage of *Spirotrichonympha.* In *Glyptotermes iridipennis,* they (1927) put into the life cycles of *Devescovina hilli, Trimitus* stages and "young stages" that I later (1938*b*) described as a separate species, *Foaina delicata.* In a species of *Kalotermes* from Lifou in the Loyalty Islands, they (1929) included under *Devescovina pruvoti* minute *Trimitus* stages, avicular forms (*Opisthomitus*), young stages of the *Devescovina* type, and large forms which reach a length of 75$\mu$.

Duboscq and Rose (1932) described a cycle in *Tryanophis grobbeni* in which there are stages differing markedly in morphology. The typical flagellates are found in the gastrovascular cavity of siphonophores. On the external surface of the pedicel of the somatocyst there occur gregariniform bodies with no trace of flagella, costa, or blepharoplast. The authors believed that the flagellates traverse the wall of the pedicel, become fixed to its external surface, and are transformed into these bodies. They stated, but did not prove, that these become encysted, detach, become free in the water, and undergo nuclear multiplication. Spirochetoid stages are said to be produced, and to occur in the gastrovascular cavity along with typical flagellates.

According to Grassé (1926), the small *Proteromonas lacertae,* in the course of its cycle, develops multiplicative cysts which may reach a diameter exceeding 75$\mu$. The flagellates supposedly resulting from multiple fission in these cysts do not, however, differ in any essential way from the typical flagellates which multiply by binary fission.

The transformations undergone by Trypanosomatidae are well known; structural features characteristic of different genera are found in the life cycle of one species. The differences, however, are almost solely in the position of the kinetoplast, accompanied by the flagellum. McCulloch's description of the life cycle of *Crithidia leptocoridis* (1915) mentioned large plasmodial masses in which "merozoites" were formed by multiple fission. In the life cycle of *Crithidia euryophthalmi* she described (1917, 1919) somatellae in process of multiple fission to form merozoites; and also "endogenous budding" in which the nucleus multiplies within the body of an elongate flagellate the flagellum, blepharoplast, and parabasal of which remain intact and in place, each resulting nucleus becoming the center of a minute zoöid of the *Leishmania* type. The extranuclear organelles of the zoöid are "formed as outgrowths from the nucleus," but a complete series of stages showing development of a "bud" into a typical crithidial form were not found. Multiple fission was also reported in this paper as occurring within epithelial cells.

A description of a life cycle, to be complete, must include an account of the methods of reproduction and, if there are markedly different stages, a demonstration of the existence of transitional forms. Most accounts of complex cycles in asexually reproducing endozoic flagellates with a single host have failed, either entirely or in part, to meet these requirements. Duboscq and Rose did not describe the process of reproduction in any stage of *Trypanophis,* and did not demonstrate convincingly the transition between spirochetoid forms and typical flagellates, between flagellates and gregariniform stages, or between the last and spirochetoids. Grassé was able to find out very little concerning nuclear multiplication in the pseudocysts of *Proteromonas.* McCulloch was unable to supply a convincing account of the multiplicative processes in endogenous budding; she believed that the nucleus repeatedly constricts or buds off portions, which is improbable.

In the present work I am concerned with the existence or absence, in devescovinid flagellates, of comparable cycles involving stages differing in the characteristics used in classifying species. No one has demonstrated the existence of any method of reproduction other than binary fission in these flagellates. I have studied in many species thousands of instances of such division. Duboscq and Grassé, however, did not describe division in any of the devescovinids which they have investigated.

The existence of transitional forms, for which they contended, is not supported by critical and detailed consideration of the morphology of the flagellates. Series can, in some degree, be found in body size, and flagella often show no great differences. But in the parabasal, axostyle, nucleus, and cresta there are means of separation that Duboscq and Grassé failed to note correctly. *Foaina* and *Devescovina* differ markedly in nuclei, axostyles, and parabasals, and can very easily be distinguished. *Tricercomitus* has no cresta, which is redifferentiated before the completion of binary fission in devescovinids. Duboscq and Grassé (1927) failed, in the so-called young stages of *Devescovina hilli*, to describe or figure the cresta, which is conspicuous in my material (1938*b*). There is, however, much more similarity between the larger and smaller devescovinids of *Glyptotermes iridipennis* in crestas, nuclei, and axostyles than exists between *Foaina* and larger devescovinids of most termites. Therefore, a study of this faunule without the aid of comparative material would be more likely to lead to misinterpretation than would almost any other.

For the most part I have encountered no difficulties necessitating arbitrary decisions in distinguishing the several species of Devescovininae described in this paper from single hosts, nor have those who have assisted me. The studies reported in this series of papers have clearly shown the desirability of avoiding confusion by treating forms markedly different morphologically as different species, in the absence of proof that there are methods of reproduction that could give rise to such different forms, and that carefully authenticated transitional series exist.

## Devescovina Foà

*Devescovina* Foà, 1905, Atti R. Accad. Lincei, (5) 14, sem. 2:546 (type species *D. striata* Foà).—Janicki, 1915, Zeitschr. wiss. Zool., 112:633.—Kirby, *partim*, 1926, Univ. Calif. Publ. Zoöl., 29:103.—Bernstein, *partim*, 1928, Arch. Protistenk., 61:27.

*Diagnosis.* Body elongated, usually pointed posteriorly; length in known species 20–80μ, rarely more, range of averages 27–62μ; width 3.5–38μ, range of averages 5.5–30μ; three slender anterior flagella about the length of the body; one trailing flagellum, which ranges from a slender cord to a band 3μ wide, about 1 to 1½ times body length; cresta length, except in *D. elongata*, 2.3–13μ, anteromedial edge 1.5–3.5μ; parabasal body spiraled around trunk of axostyle or posterior part of nucleus ½ turn to 5 turns, rarely more; parabasal usually simple, without a branch or distal element, except in occasional specimens and in *D. fissa;* capitulum of axostyle simple, except in *D. insolita;* trunk of axostyle usually tapering to a filamentous posterior end completely enclosed in the cytoplasm, occasionally stouter for most of its length, exceptionally projecting; nucleus ellipsoidal or ovoidal, longer diameter usually in the direction of the longitudinal axis of the body, membrane well defined, chromatin in large and small readily staining granules in a central chromatin mass, peripheral nucleolus, clear space under membrane frequently present in prepared material; rod-shaped microörganisms present on the surface of all known species, usually on all the body except the most anterior part, forming apparent longitudinal striations; spirochaetes adherent to parts of, or all, the body in some species, absent in others.

## GENERAL MORPHOLOGY

The body of *Devescovina* is circular in cross section and is gradually tapered to a point posteriorly. The broadest part is often anterior to the middle. A sharp distinction between a rounded anterior part and a slender caudal projection, as was described by the writer in *D. lemniscata,* is not normal. Larger specimens may be stouter in form, with a less gradual taper. These, also, normally have a pointed posterior end; but in preparations large specimens are often broadly rounded posteriorly. Janicki (1915) described and illustrated such a rounded end in the larger specimens of *D. hawaiensis,* and his figure (pl. 13, fig. 2) has been reproduced in several compilations (Wenyon, 1926; Doflein-Reichenow, 1927–29; Calkins, 1933; Prenant, 1935). Its shape is, however, not representative of either the species or the genus.

The anterior end is extended into the flattened papilla. The anterior edge of this usually forms an uninterrupted curve with the dorsal edge of the body, but ventrally the papilla is pointed (fig. A). The body, consequently, is extended into a point on one side. Often the papilla is not seen as such, because of its position, although it is a constant structure. I mistakenly regarded it as an inconstant protuberance in *D. lemniscata* (1926), and it was not mentioned or figured in *D. elongata* by Bernstein (1928), nor in *D. paralemniscata* by Calkins (1936). Janicki (1915) and Grassi (1917) seem to have understood the structure, though the former omitted it in most of his figures. I have seen it in all species in this study, and usually have figured specimens that show it. It has been noted that at times the papilla is motionless and is turned back against other parts of the body so that the point is not distinguishable, and that that is the position commonly taken when the flagellates die. It is because of this fact that in the majority of fixed specimens the papilla cannot be distinguished. It is, of course, simply a part of the cytosome, from which it may or may not be distinguishable. I have studied the movements of the papilla in *Devescovina lemniscata* (p. 61).

As in other Devescovininae, the flagella leave the blepharoplast and pass in two roots along the anterior edge of the papilla to its tip. They then seem to leave the tip, but the more proximal parts are not intracytoplasmic. In many fixed specimens the anterior flagella have been observed detached for part of, or all, the distance to the blepharoplast, leaving the papilla formed as usual.

The blepharoplast group is more compact than in some Devescovininae. In suitably stained material it is visible as a mass of small or moderate size at the very edge of the body anterior to the cresta. It is most distinct in material that is too much overstained with iron-haematoxylin for study of general structure. There also appear to be some differences in size, with depth of staining, as if there were some matrix substance surrounding the blepharoplast group and composed of material that destains more readily. It is probable that in *Devescovina* the blepharoplast is never a simple granule, though it often appears to be. Very frequently, when well stained, it may be seen clearly as an aggregation of several granules, probably not more than four or five, which are large enough to lie adjacent to one another in the mass. Their presence can usually be recognized by the irregularity of outline of the mass. When destaining is carried further, each granule may seem smaller, and the whole appears as a vaguely defined group. In *Devescovina* there is no group of distinctly separated granules, as in *Caduceia nova* (Grassi, 1917; Kirby, 1936), *Macrotrichomonas pulchra* (Grassi, 1917; Kirby, 1938*a*) and many other devescovinids.

Janicki (1915) reported the compound character of the blepharoplast group, but he represented that structure as being much larger than it actually is. I have not been able to verify, in recently studied material, Janicki's report of a membrane surrounding the group of granules; or my own report (1926) of a similar structure in *D. lemniscata.* Calkins (1936) noted that the blepharoplast "contains from one to three deeply-staining granules" in *D. paralemniscata* (=*D. striata*).

A filament (fig. A; pl. 4, fig. 34) from the blepharoplast to a near-by point on the nuclear membrane has been observed in many species, and probably sufficient searching would reveal it in all species. This is the structure named the nuclear rhizoplast in *Devescovina lemniscata* (Kirby, 1926). My more recent observations have failed to reveal a centrosome (centriole) at the end of this filament on the nuclear membrane, as was supposed to exist in *D. lemniscata* at that time, and as was also described by de Mello and de Brito (1929). It is unlikely that there is such a granule.

All species of *Devescovina* studied by me have three slender anterior flagella about as long as the body (pl. 5, fig. 39; pl. 7, fig. 49). These were correctly observed by Foà in *D. striata* and by Janicki in *D. hawaiensis.* Grassi (1917) wrote of at least two anterior flagella in *D. glabra,* but some of his figures show three. Calkins (1936) stated that in *D. paralemniscata* (= *D. striata*) the anterior flagella are only about one-third the body length. However, I have seen no flagella relatively as short as this on species of *Devescovina* from any termite, including the host of Calkins' species.

In most species of *Devescovina* the flagella pass directly into the blepharoplast group. *D. insolita* is an exception in that the two roots of the anterior flagella end as stout fibrils a short distance from the blepharoplast, to which they are connected by fine fibrils (fig. F, 1). In *D. tendicula,* one root enters the blepharoplast directly, but the other ends at an enlargement or granule near it and is connected to it by a fine fibril. These peculiarities of the two species are constant characteristics and present a situation like that in certain more advanced devescovinids.

The trailing flagellum differs in diameter in different species, ranging from little more than that of an anterior flagellum (pl. 1, fig. 2) to that of a broad ribbon (pl. 6, fig. 45). The tendency for it to become broadened and flattened is marked in the genus. However broad it may be, it always is reduced to a filament at its attachment to the body and in its terminal portion. There is some variation in its breadth in different individuals of the same species. Sometimes there are differences in flagellates assigned to the same species from different host termites. Thus in *D. glabra* in different hosts the flagellum may be a cord or a narrow band; and in *D. lemniscata,* although it is usually a ribbon, there is some difference in the breadth characteristic of the majority of the flagellates in different hosts. To some degree this variation within a species in different host species is due, of course, to the species limitations the writer has chosen to recognize. If small differences in the trailing flagellum were used to separate species or varieties, the taxonomic situation would be very complicated; nevertheless, differences of the proper kind are of great value in distinguishing species.

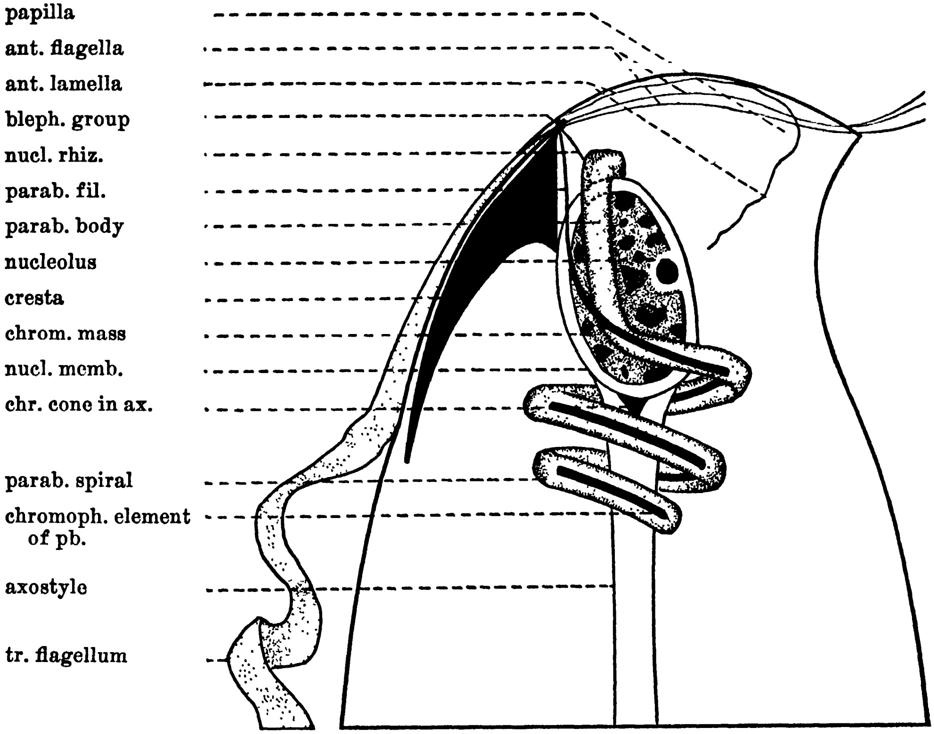

Fig. A. Diagrammatic figure of the anterior part of *Devescovina,* based on *D. lemniscata.* × 4700. Structures shown: *papilla,* a mobile, flattened structure constituting the anterior end; three *anterior flagella,* which appear as two roots insecurely adherent to the surface of the papilla; *anterior lamella,* in the papilla and ventrally extending posteriorad, probably the edge of the capitulum of the axostyle; *blepharoplast group,* a group of four or five granules; *nuclear rhizoplast,* a filament from the blepharoplast group to the nuclear membrane, here passing under the anterior end of the parabasal body; *parabasal filament,* anteriorly separated from the longitudinal part of the other substance of the parabasal body, and passing separately anteriorad to connect with the blepharoplast; *parabasal body,* label on the longitudinal part, which is applied to the surface of the nucleus and turns ventrally on the anterior end of the nucleus, and is not connected directly to the blepharoplast group; peripheral *nucleolus* and *chromatin mass,* with a space (possibly owing to shrinkage) between it and the *nuclear membrane; cresta,* flattened, located at origin on the dorsal side of the body; *chromatic cone,* located in the anterior part of the trunk of the axostyle; *parabasal spiral,* turned around the trunk of the axostyle; *chromophile element of parabasal,* continuous with the filament, often broadened to a band; trunk of *axostyle; trailing flagellum,* which in some species is a broad band as shown, but varies in size in different species.

The trailing flagellum is usually somewhat longer than the body, often about 1½ times as long (pl. 7). It is never very much shorter than the body as in certain larger devescovinids, and does not reach several times the body length as in certain species of *Foaina.* Usually the trailing flagellum is longer than the anterior flagella. Because of the uniformity in this respect among species of the genus, I have seldom, in the following account, recorded the length of the trailing flagellum.

Relative to the size of the body, the cresta is of small to moderate size. The longest cresta is in *D. lemniscata,* in which it averages less than one-fourth the average length of the body. This is a contrast to the situation in certain species of *Foaina* and *Metadevescovina,* in which the cresta is as long as the body. Its form is subtriangular, with the anteromedial edge shortest in most species; but there is an exception to this in *D. lepida* and *D. arta,* in which the posteromedial edge is the shortest. Within a species there is a limited degree of variation in the size of the cresta, but in shape and proportions there is so much constancy that the cresta is of much value for taxonomic purposes. Motility of the cresta has not been observed in *Devescovina.* The relationship of the cresta to the trailing flagellum, especially with respect to the insecure nature of the adherence of the flagellum to the surface above the external edge of the cresta, is discussed under *D. lemniscata* (p. 62).

The parabasal apparatus is a single body coiled around the trunk of the axostyle in a laeotropic spiral (pl. 4, fig. 35). The number of turns is usually small in flagellates of this genus; it is sometimes less than one and seldom exceeds five. The turns of the spiral are always rather close together, never loose and much drawn out as in certain species of *Metadevescovina* and *Caduceia,* but there are differences between species in the degree of closeness of the turns. Although within a species there is variation in the number of turns of the parabasal body, the limits of variation are of taxonomic value.

The anterior, longitudinal part of the parabasal body lies against the nuclear membrane. Often it extends along the anterior surface of the nucleus beyond the point situated closest to the blepharoplast, as was previously noted (Kirby, 1938*b*), and there is no connection between this part and the blepharoplast. In many species, as previously noted (Kirby, 1937*c*), the parabasal filament separates from the main substance more posteriorly, even near the point where the parabasal bends transversely, and continues separately to the blepharoplast (fig. A; pl. 4, fig. 34).

Usually the parabasal body of *Devescovina* lacks any branching or distal outgrowth; among Devescovininae in this genus that development is least in evidence. It is not absent, however. A ramus or branch of the parabasal body has been observed in a few individuals of *D. glabra* (pl. 2, fig. 14) and *D. transita;* and the presence of one ramus is a characteristic of *D. fissa* (fig. B, 5, 6; pl. 2, figs. 15–19).

The parabasal body of *Devescovina* usually stains uniformly with Delafield's haematoxylin, although sometimes a heterogeneity in the form of small, clear vesicles is apparent. In no species does the parabasal show the structure of well-defined granules or blocks that is conspicuous in certain Devescovininae, especially in some species of *Metadevescovina* (Kirby, 1931*b*).

The axostyle in *Devescovina* is comparatively simple. In most species the trunk tapers to a filamentous posterior part enclosed within the cytoplasm. In many species, for a large part of its length the axostyle is sinuous (pl. 6, fig.

41); certainly in these species it is not a rigid, form-maintaining structure. When the trunk of the axostyle is longer than the cytosome, typically instead of projecting it is recurved. What sometimes appears to be a projecting axostyle in *Devescovina* is usually axostyle plus a sheath of cytoplasm, left after loss of parts of the cytosome. This is the explanation of the supposed long, projecting axostyle in certain specimens of *D. lemniscata,* which I have previously described (1926). In *D. hawaiensis* and *D. exilis* there are one or two rings surrounding the trunk in its posterior part. These have not been observed in other species.

While an axostylar trunk of this type is characteristic of *Devescovina,* there are some atypical forms. In certain species (*D. robusta, D. vestita, D. parasoma*) the trunk is not reduced to a filament within the cytoplasm, and is stout enough for almost all its length so that it is not sinuous (pl. 5, figs. 36, 37). In *D. vestita* and *D. parasoma* the slender posterior end of the axostyle frequently projects for a few microns beyond the posterior end of the body, but there is no cusplike enlargement.

The capitulum of the axostyle is typically a simple, flat expansion. A haematoxylin-staining lamella which is present in the papilla of many if not all species is probably an edge of the capitulum. The lamella passes near the anterior edge of the papilla, close to the roots of the anterior flagella. At the tip of the papilla, or near it, it turns posteriorly. The apparent end of the lamella sometimes comes in contact with the nuclear membrane, but more frequently it is free and variable in position.

A capitulum of a different type has been seen only in *D. insolita.* In that species it is an elaborate, broadly expanded structure (pl. 3, figs. 26, 27), unusual for *Devescovina,* rather suggesting the situation in certain species of *Metadevescovina.* In other respects, however, the species clearly belongs in the genus *Devescovina.*

Peripheral to the anterior lamella, especially in its longitudinal part, a clear area is frequently present in the cytoplasm. Often this is rather broad. It suggests a cytostome, as that is described in some trichomonads, but beyond it is the unmodified wall of the body, often with a layer of granular cytoplasm beneath it. The existence of the clear area may be the result of disturbance of the region by activity of the papilla, which must cause the capitulum to change constantly in position.

An elongated group of small granules alongside the nucleus constitutes the chromatic shield (fig. B, 2; pl. 2, figs. 20, 21), which seems to be a separate structure from the capitulum of the axostyle. It is present in many species, but apparently not in all.

A suspensorial lamella, which was first described by Janicki (1915), is present in *D. hawaiensis,* under which heading it is discussed below (p. 65). Certain material of *D. hawaiensis* was especially favorably prepared for study of this structure (pl. 9, figs. 62, 63, 65); it was not seen so well in other material of that species. It is clearly an independent structure.

The nucleus of *Devescovina* is ellipsoidal or ovoidal in form, with no irregularity of outline, and its longer diameter is usually in the direction of the longitudinal axis of the body. The blepharoplast is anterior to it, usually not in the central axis but toward the dorsal side. Janicki's accurate description of the nucleus of *D. hawaiensis* applies in general to the nucleus of all members of the genus. The nuclear membrane is well defined. The chromatin material, which is dispersed in large and small irregularly arranged granules, stains deeply. At some point on the periphery of the mass there is usually present a nucleolus (Binnenkorn) surrounded by a clear area, as in other Devescovininae. Between the membrane and the chromatin mass a clear space is present in most fixed material and has been observed in living specimens of *D. lemniscata* from *Neotermes insularis.*

As stated above (p. 13), I agree with Janicki's interpretation of this clear space as the result of shrinkage under the influence of reagents. The nucleus of *Devescovina* is particularly predisposed to this shrinkage. In certain material, however, the space may not be present; this is often true of material fixed in Flemming's fluid. The predisposition to the development of such a space under the action of reagents, if not the presence of the space itself, is a marked characteristic of the species of the genus *Devescovina.*

Posterior to the nucleus, in or on the trunk of the axostyle, there is in many species of *Devescovina* a conical structure the base of which is apparently applied to the nuclear membrane. This structure often stains as deeply as the nucleolus with iron-haematoxylin, that is, more deeply than the chromatin itself. In some species, as in *D. cometoides,* a conical structure comparable in position is clearly a pointed prolongation of the chromatin mass; even when the shrinkage space under the membrane is present, it is connected to that mass. In other species, when the shrinkage space is present, the conical structure is separated from the chromatin mass, and it seems to be separated from the nucleus.

Particles of wood are present in the cytosome of all species described here except *D. elongata.* Usually this wood is evenly distributed in the cytoplasm posterior to the nucleus and parabasal body, but in *D. tendicula* and *D. vittata* small wood particles are often accumulated in a dense mass just posterior to the nucleus so that two distinct regions are differentiated (fig. D, 4, 5; pp. 38, 54).

The body surface of all species of *Devescovina* described in this paper constantly bears rodlike microörganisms applied by their full length in a direction that in general is more or less longitudinal. Usually they are present on all parts of the body except the anterior end, and under normal circumstances no specimen is found without them. They are restricted to the posterior part of the body in *D. robusta* (pl. 3, fig. 25) and *D. insolita* (fig. F, 3). They seem to be of the same type on almost all species. Those on *D. elongata* (pl. 1, fig. 1) are markedly shorter and relatively stouter than usual, clearly being of a different type; those on *D. vestita* (pl. 5, fig. 37) are somewhat shorter, stouter, and more irregular in alignment than usual.

These adherent microörganisms were mistakenly regarded as pellicular striations by Foà (1905) on *D. striata,* by Janicki (1915) on *D. hawaiensis,* by me (1926) on *D. lemniscata,* and by Bernstein (1928) on *D. elongata.*

Grassi (1917) did not mention the rods on *Devescovina glabra,* and Calkins (1936) failed to see them on *D. paralemniscata* (=*D. striata*), but I have found them on both those devescovinids. Their detailed structure and the evidence that they are not pellicular structures are discussed in a later section of this monograph (see also Kirby, 1941). Although they are not part of the flagellates, their presence is so constant as to be a characteristic of *Devescovina;* but of course if any species should be found without them, it might still, on the basis of other characteristics, be included in *Devescovina.*

Adherent spirochaetes are usually or always absent from some species. None were found, for example, on *D. lemniscata* in eighteen of its nineteen hosts, or on *D. striata* in its five hosts. Spirochaetes were not regularly adherent to six more species. On other species the presence of spirochaetes is characteristic. These are always of the same type and are distributed, usually, in the same way. Often they are present in a group on the region of the papilla (pl. 2, fig. 8). *D. cometoides* bears such a group, for example, in all its hosts, with spirochaetes present elsewhere on the body in some hosts but not in others, and five other species of *Devescovina* have spirochaetes mainly or entirely on the anterior end. In some species spirochaetes are distributed over the whole surface of the body; one, *D. vestita,* is unusual in that the microörganisms are absent only from the anterior part (pl. 5, fig. 36). The spirochaetes on *Devescovina* usually are relatively long, with a length often in the neighborhood of 10$\mu$.

## DISTRIBUTION

The twenty species of *Devescovina* described in this paper have been found in a little more than half of approximately 125 host species, in the three lower families of termites, which have been examined. The number of hosts recognized is only an estimate because many of the termites have not yet been studied and have therefore been grouped in a preliminary manner according to the character of their flagellate faunules. That method may fail to separate certain distinct species. Only eleven of the termites, one of which contained *Devescovina,* did not belong in the Kalotermitinae. In that subfamily of termites, *Devescovina* is widespread. Nine species have only one host each; five have two hosts, and two of these five may actually be the same species of termite. Six species of *Devescovina,* that is, less than one-third the total number, occur in about three-fourths of the termites that harbor the flagellate. *Devescovina lemniscata,* which has nineteen hosts, and *D. glabra,* which has fifteen, are the most widely distributed species. *D. cometoides* and *D. lepida* have seven hosts each, *D. parasoma* six, and *D. striata* five.

Eleven of the hosts contained two species each, the rest only one each. The occurrence of only one species of this genus in a host is the rule, whereas in *Foaina* there are two or three species in 44 per cent of the hosts. In four of the termites both *D. lemniscata* and *D. cometoides* are present; three of these are *Cryptotermes* of the *dudleyi* type, possibly all actually *dudleyi,* and the fourth (*"Coptotermes heimi,"* de Mello) is unknown. The difference between the two flagellates is as great as that between almost any two species of *Devescovina;* there is no question in my mind that they are distinct. In one termite *D.*

*cometoides* is associated with *D. glabra,* in another with *D. parasoma,* and in two others with *D. transita.* Although some taxonomic difficulty is presented by these three species, *D. cometoides* is clearly distinct from them all. The other associations are *D. lemniscata* with *D. glabra, D. lepida* with *D. arta,* and *D. exilis* with *D. hawaiensis.* The relationship between the last-named two species is discussed in the account of *D. exilis* (p. 49).

## TAXONOMY

Only six of the twenty species described in this paper have previously appeared in the literature: *D. striata, D. hawaiensis, D. glabra, D. lemniscata, D. cometoides,* and *D. elongata.* It has been necessary to exclude from the genus certain species that were placed in it by their original authors or later workers. *D. nova* Grassi, 1917, and *D. stereociliata* Grassi, 1917, have been removed from the genus, after study of specimens, the former being placed in *Caduceia* (Kirby, 1936) and the latter in *Metadevescovina. Devescovina polyspira* Lewis, 1933, has been placed in *Metadevescovina. D. hilli* Duboscq and Grassé, 1926, is quite unlike species of *Devescovina* in the parabasal apparatus, and I have removed it from that genus (1938*b*). The original species also included *Foaina delicata* Kirby, described in the above-mentioned paper. *Devescovina pruvoti* Duboscq and Grassé, 1929, is a complex of several flagellates. The large "adult" forms belong in the genus *Caduceia.* The so-called "young" forms probably include a species of *Devescovina,* represented by their figure 2, *Tricercomitus,* and possibly *Foaina,* but these forms were too adequately described for further consideration here. *D. damanensis* de Mello and de Brito, 1929, is a synonym of *D. lemniscata,* and their *D. kirbyi,* described in the same paper, is *Foaina nova. D. paralemniscata* Calkins, 1936, is a synonym of *D. striata.*

## KEY TO THE SPECIES OF DEVESCOVINA

**1. Trailing flagellum not band-shaped or, if so, very narrow ........................ 2**
**Trailing flagellum usually markedly band-shaped ................................ 11**
**2. Cresta inconspicuous, 1 to 2μ long, with very short anteromedial edge; body form elongated ................................................ *D. elongata***
**Cresta broader anteriorly and much more conspicuous ............................ 3**
**3. Cresta length under 4μ, anteromedial and posteromedial edges about equal. *D. cometoides***
**Cresta longer than 4μ, posteromedial edge longer than anteromedial .............. 4**
**4. Parabasal body coiled around axostyle about 1 turn, with an outgrowth from the main part running along its anterior edge in most specimens ............... *D. fissa***
**Parabasal body typically unbranched ............................................ 5**
**5. Trunk of axostyle of usual form, filamentous in its posterior part, and generally completely enclosed in the cytosome ...................................... 6**
**Trunk of axostyle stouter than usual in its posterior part, often projecting from the cytosome .................................................... 9**
**6. Parabasal spiral usually with 1 turn or only a little more ...................... 7**
**Parabasal spiral frequently with 2 or more turns ................................ 8**
**7. Parabasal turned widely, in an almost complete loop, around the posterior part of the nucleus, with a sigmoid curve in its longitudinal part; nucleus 5 or more microns long ................................................. *D. tendicula***
**Parabasal spiral closer, more drawn out, turned around trunk of axostyle, without sigmoid curve, nucleus 5 or less microns long ........................... *D. coghilli***

8. Capitulum of axostyle simple, trailing flagellum a cord or very narrow band; nucleus usually less than $7\mu$ long ........ *D. glabra*
Capitulum broadly expanded anteriorly and dorsally, with a membrane passing partly around the nucleus; nucleus 7 to $8\mu$ long ........ *D. insolita*
9. Length of nucleus more than $7\mu$; surface rods restricted to posterior part.... *D. robusta*
Length of nucleus less than $7\mu$; surface rods usually on entire body except anterior end ........ 10
10. Trailing flagellum a very narrow ribbon; parabasal spiral with 3 to 4 turns in majority of specimens ........ *D. parasoma*
Trailing flagellum a stout cord; parabasal spiral usually with about 2 turns... *D. vestita*
11. Cresta length usually under $4\mu$ ........ 12
Cresta length usually more than $4.5\mu$ ........ 14
12. Posteromedial edge of cresta much shorter than anteromedial edge; trailing flagellum a broad ribbon ........ 13
Cresta of usual form, posteromedial edge at least equal to anteromedial edge; trailing flagellum a narrow band ........ *D. exilis*
13. Posterior end of parabasal tapered to a blunt point, longitudinal part of parabasal slender; body form narrow ........ *D. arta*
Posterior end of parabasal broad and rounded as usual, longitudinal part stout; body of more usual breadth ........ *D. lepida*
14. Size exceptionally large, usually few specimens less than $50\mu$ in length and $25\mu$ in width; elongated triangular cresta not narrowed so much in posterior part as usual, often bluntly pointed or truncate posteriorly ........ *D. vittata*
Size smaller; cresta, if elongated, more narrowed and sharply pointed posteriorly.... 15
15. Trailing flagellum a broad band, usually more than $1\mu$, up to $3\mu$ ........ 16
Trailing flagellum a narrow band, usually less than $1\mu$ ........ 17
16. Cresta short, less than $7\mu$, with posteromedial edge often little longer than anteromedial edge ........ *D. striata*
Cresta longer, $7\mu$ or more, reaching $13\mu$, posteromedial edge more than twice length of anteromedial edge ........ *D. lemniscata*
17. Anteromedial edge short, measuring less than $2\mu$, cresta unusually narrow; parabasal body with about 1 turn, never so much as 2 ........ *D. uniflexura*
Cresta broader, parabasal body with more than 1 turn in most specimens ........ 18
18. Parabasal in a tight, close spiral of 1¼ to 2½ turns; adherent spirochaetes... *D. similis*
Parabasal either more loosely wound or with more turns; usually no adherent spirochaetes ........ 19
19. Parabasal turns in the majority of specimens 1½ or fewer, but some up to 5; band-shaped suspensorial lamella present ........ *D. hawaiensis*
Parabasal turns rarely fewer than 1½, averaging 2 to 4; no band-shaped suspensorial lamella ........ *D. transita*

## COMPARISON OF SPECIES

In this section certain distinctions between species of the genus *Devescovina* are discussed. It is not to be supposed, however, that the points of difference between species have been exhausted here. Study of the characteristics given in the text, which have been worked out carefully from a large number of specimens, will often reveal other differences, and some other points in comparison are made in the accounts of the species. The taxonomic treatment accorded the genus has been based on repeated comparison of specimens—observations that cannot be completely represented by drawings and descriptions. Although it has been impossible to avoid uncertainty in classification of some species of the genus, one thing seems indubitable: in the hosts examined, no flagellates not included in the descriptions of *Devescovina* given here belong in the life history of described species of that genus.

Several species of *Devescovina* can easily be distinguished from all other described species: *D. elongata* by its very slender form (pl. 1, figs. 2, 3), its short narrow cresta (fig. B, 1), and the fact that the trailing flagellum is almost no stouter than an anterior flagellum; *D. fissa* by its branched parabasal body (fig. B, 5, 6); *D. insolita* by the elaborate capitulum of its axostyle (pl. 3, fig. 27); *D. robusta* by its very large nucleus (fig. B, 11) and by its stout axostylar trunk (pl. 3, fig. 25), which is not filamentous posteriorly as is usual in *Devescovina; D. tendicula* by the form of its parabasal body, which has a sigmoid curve in its longitudinal part and a wide transverse loop (fig. B, 7).

In two species, *D. lepida* (fig. C, 1) and *D. arta* (fig. B, 16), the cresta is very short and has a unique form, the posteromedial edge being much shorter than either of the other two edges, which are about equal in length. *D. arta* is usually much more slender than *D. lepida,* but differentiation rests mainly on the parabasal body. The slender anterior longitudinal part of the parabasal of *D. arta* (pl. 6, fig. 42) is unusual in devescovinids, but the existence of the characteristic has been verified by repeated observations.

Each of the seven species just mentioned has at least one characteristic uniquely different from those of the remaining thirteen species of *Devescovina.* Among these thirteen, a greater amount of systematic difficulty is encountered. The characteristics used for taxonomic distinction all vary within certain species within broader limits than have been taken to separate some of the species, and, unavoidably, personal judgment enters into the systematic treatment of the group.

Very short crestas, the posteromedial edge of which is little if any longer than the anteromedial edge (1–1½ times), occur constantly in *D. cometoides* and *D. exilis.* The trailing flagellum of *D. exilis* is a very narrow band (pl. 5, fig. 39), somewhat different from the cordlike trailer of *D. cometoides* (pl. 1, fig. 5). The parabasal body is wound more closely and often for a greater number of turns in *D. cometoides* than in *D. exilis;* furthermore, in the latter species the terminal part of the single turn is often extended in a straight line.

*D. striata* often has a similarly shaped though larger cresta (fig. C, 6). The body commonly has a broader form, but the species is readily distinguished by the broad, band-shaped trailing flagellum, which is a characteristic ribbon (pl. 7, fig. 49). A similar broad trailing flagellum is characteristic of *D. lemniscata,* as well as of *D. lepida* and *D. arta,* which have previously been mentioned and are readily to be distinguished from the others by the unique form of the cresta. In *D. lemniscata* the length of the cresta (fig. C, 5) is markedly increased; the anteromedial edge is the same as in *D. striata,* but the minimum length in the species usually surpasses the maximum in *D. striata.* The maximum length in *D. lemniscata,* 13$\mu$, is the greatest in the genus. The cresta length is the only important point of difference between the two species, however, and sometimes, as in the flagellate in *Cryptotermes fatulus,* distinction is not so clearcut as usual. (p. 59).

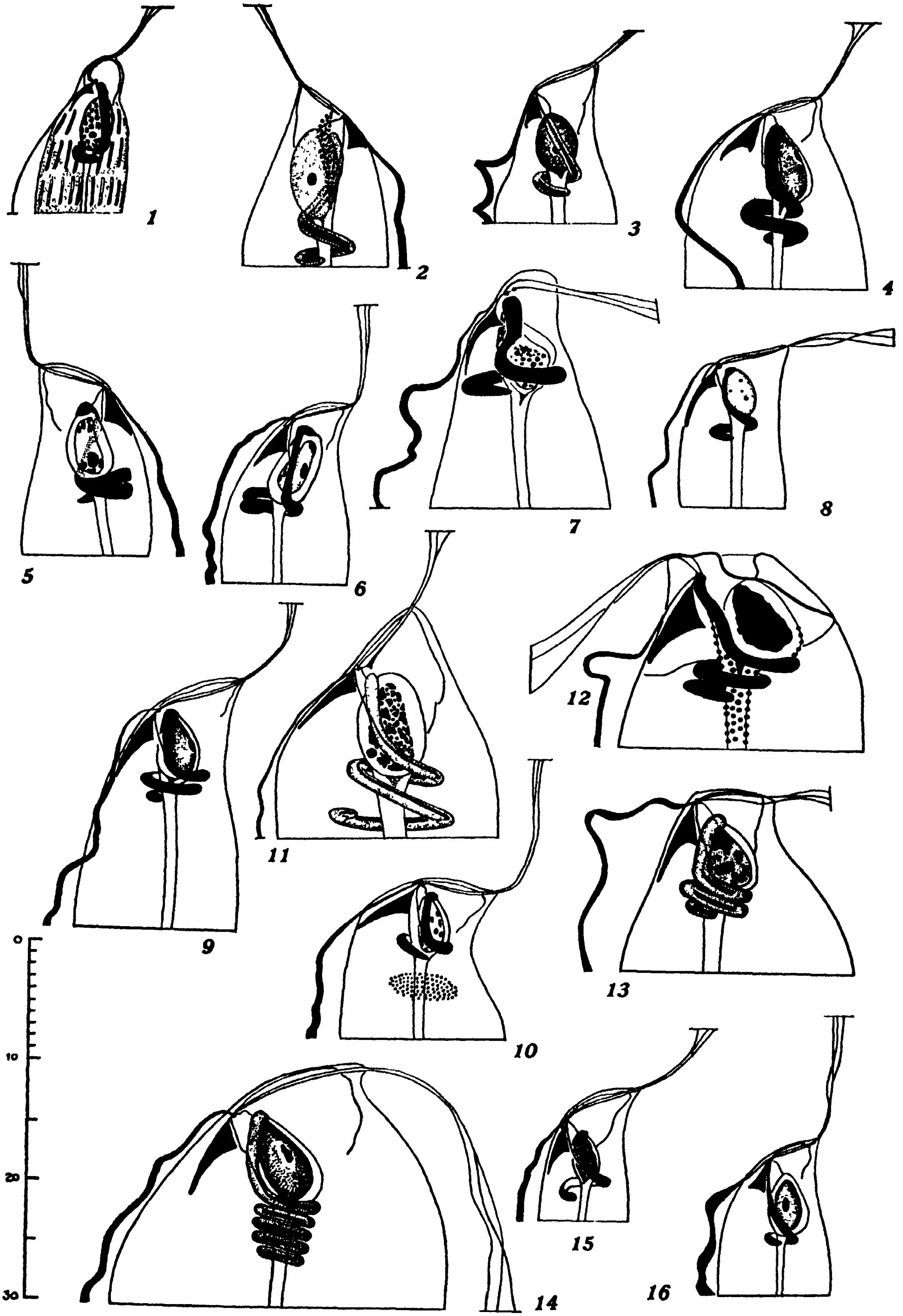

Fig. B. Species of *Devescovina*. 1. *D. elongata* Bernstein from *Anacanthotermes ochraceus*, Egypt, showing adherent rods (bacteria) on surface. 2–4. *D. cometoides* de Mello and de Brito; 2, 3, from *Kalotermes repandus*, Fiji Islands; 4, from *Cryptotermes dudleyi*, Panama. 5, 6, *D. fissa* sp. nov. from *Procryptotermes* sp. nov., Réunion. 7. *D. tendicula* sp. nov. from *Kalotermes jeannelanus*, Tanganyika Territory. 8. *D. coghilli* sp. nov. from *Cryptotermes merwei*, Natal. 9, 10. *D. glabra* Grassi; 9, from *Cryptotermes* sp. T-4303, Madagascar; 10, from *Neotermes meruensis*, Kenya Colony. 11. *D. robusta* sp. nov. from *Neotermes erythraeus*, Eritrea. 12. *D. insolita* sp. nov. from *Neotermes* sp. T-2012, Tanganyika. 13. *D. vestita* sp. nov. from *Glyptotermes niger*, Java. 14. *D. parasoma* sp. nov. from *Neotermes tectonae*, Java. 15. *D. exilis* sp. nov. from *Neotermes connexus*, Hawaii. 16. *D. arta* sp. nov. from *Glyptotermes angustus*, Panama. 2, 3, 15, × 1800; others and scale, × 1750.

Of the nine remaining species, in which the trailing flagellum is a narrow band or a cord, *D. transita* is closest to *D. lemniscata.* In *D. transita* the cresta and parabasal body do not differ from those structures in certain material of *D. lemniscata,* but the band-shaped trailing flagellum (fig. C, 10–13) has a breadth much less than that usual in *lemniscata* (fig. C, 5). In some material from *Cryptotermes cynocephalus,* in fact, it was no more than a cord.

A similar narrow band-shaped trailing flagellum is present in *D. similis* (fig. C, 7), distinguishing it from *D. lemniscata* and *D. striata. D. similis* differs from *D. transita* in the cresta and parabasal body. The cresta averages about 2μ shorter than that of *D. transita,* being only a little greater than that of *D. striata.* The parabasal body often has markedly fewer turns than that of *D. transita*—an average of 2 with a maximum of 2½, as compared to an average of 3¾ with a maximum of 5½ in *D. transita* on some slides from *Glyptotermes* T-4571 of Java; but this is not always so, as a flagellate from *Cryptotermes cynocephalus,* with the same smaller average number of turns as in *similis,* has been identified with *D. transita* (p. 66).

*Devescovina hawaiensis* (fig. C, 8) also has a much narrower band-shaped trailer than *D. striata* and *D. lemniscata.* The trailing flagellum is narrower, in general, than that of *D. transita.* The suspensorial lamella (p. 65) is to be found only in *D. hawaiensis,* so far as my observations have gone. It is improbable, however, that it is peculiar to *D. hawaiensis;* other preparations may have been inadequate to demonstrate it, and it may be represented in other species by at least a filament. The cresta averages somewhat shorter than that of *D. transita* and *D. lemniscata,* but its anteromedial edge is as long or longer. There is a rather constant difference in shape, the concavity of the anterior part of the posteromedial edge (pl. 9, figs. 62, 63) being more marked. In length the cresta only a little exceeds, on the average, that of *D. similis,* and many specimens are alike; the resemblance between the two in cresta and trailing flagellum is close. In addition to the presence of the suspensorial lamella, *D. hawaiensis* differs markedly from *D. similis* and the other species named in this paragraph in the form of the parabasal body. The parabasal is closely wound around the trunk of the axostyle in those species, but especially in *D. similis,* even when the spiral is short; in *D. hawaiensis* the majority of specimens have 1½ turns or fewer, and the loop is characteristically broad and open (pl. 9, fig. 62).

*Devescovina vittata* resembles some of the foregoing species in trailing flagellum and length of cresta, but differs from them all in shape of cresta (fig. C, 2, 3). The anteromedial edge of this is a micron or so longer than in the others; the taper is gradual, without the deep inner concavity of the anterior part that is characteristic of *D. hawaiensis;* and the posterior end is bluntly pointed or truncate, instead of being sharp pointed. The most noteworthy characteristic of *D. vittata* is its large size and broad form. The length range is overlapped by the larger forms of most other species, and two others, *D. tendicula* and *D. insolita,* have minimum lengths also between 40 and 50μ; but the average width is more than 10μ greater than in any other species except *D. robusta,* which comes within 8μ of it. The nucleus of *D. robusta*

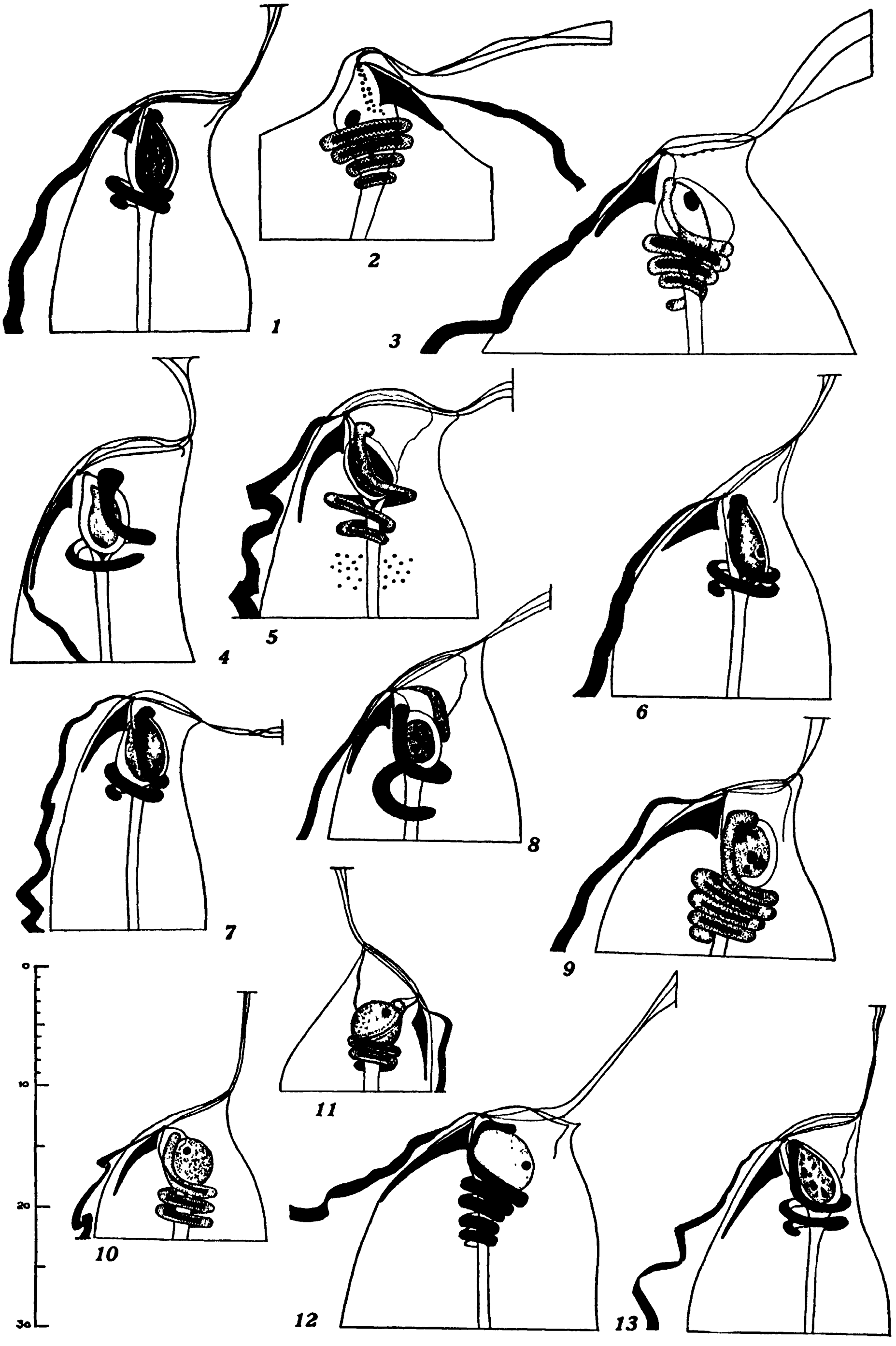

Fig. C. Species of *Devescovina*. 1. *D. lepida* sp. nov. from *Calcaritermes brevicollis*, Panama. 2, 3. *D. vittata* sp. nov. from *Kalotermes* sp. nov. T-3025, Tanganyika Territory. 4. *D. uniflexura* sp. nov. from *Kalotermes perezi*, Costa Rica. 5. *D. lemniscata* Kirby from *Cryptotermes* sp. T-1013, Tanganyika. 6. *D. striata* Foà from *Cryptotermes darwini*, Galápagos. 7. *D. similis* sp. nov. from *Cryptotermes* sp. nov. T-4459, Madagascar. 8, 9. *D. hawaiensis* Janicki from *Neotermes connexus*, Hawaii. 10–13. *D. transita* sp. nov.; 10, 11, from *Kalotermes repandus*, Fiji Islands; 12, from *Glyptotermes* sp. nov. T-4571, Java; 13, from *Cryptotermes cynocephalus*, Java. 5, 10, 11, × 1800; others and scale, × 1750.

averages 2 by 1½μ larger, and the parabasal body and axostyle are quite different. Large forms of *D. hawaiensis* closely resemble *D. vittata,* but there is a constant difference in the shape of the cresta, and no smaller forms are present in *D. vittata.*

*Devescovina glabra* has a trailing flagellum that, in various host infections, varies from a cord to a narrow band. It is possible that some forms assigned to it in the following account should really be separated from it, as there are differences among them as great as have been used to separate some species. There is, for example, a difference of 2.5μ in the average length of the cresta (5–7.5), and more than 3μ in the maximum length (5.5–8.8). The absence of the broad ribbon trailer eliminates *D. lemniscata* and *D. striata.* Size, as well as shape of cresta, eliminates *D. vittata. D. hawaiensis* has the suspensorial lamella and a differently formed parabasal body, as is discussed in the second preceding paragraph. The resemblance of *D. glabra* to *D. similis* and *D. transita* is closer.

In *D. similis* the band shape of the trailing flagellum is more pronounced than in *D. glabra,* even in *D. glabra* from *Cryptotermes havilandi* and *Cryptotermes* sp. from Beira, in both of which it is a band. The parabasal body is wound tightly and closely in *D. similis,* in which it differs from *D. glabra* in those two hosts. The nucleus of *D. similis,* even in Schaudinn-fixed material, had no clear space between the membrane and the chromatin mass, and the pale nuclear contents with a few granules differed from the more deeply staining mass in the nucleus of the *D. glabra* examined. Distinction of the species, like that of some others, is not beyond doubt, however, as examination of more material from various colonies of the hosts might possibly invalidate the characteristics used.

*D. transita* differs from *D. glabra* in ways similar to those of the species just mentioned, as is discussed at more length in the account of *D. transita* (p. 66).

*Devescovina parasoma* (fig. B, 14) is close to *D. glabra.* The narrow band-shaped trailing flagellum is like that in some material of *glabra.* The cresta is shorter than in the type of that species, but *D. glabra* in some hosts has an equally short cresta. The trunk of the axostyle is stouter (pl. 4, fig. 32) in its posterior part than that of *D. glabra,* so that rarely is it sinuous, as the filamentous terminal part in *D. glabra* (pl. 2, fig. 12) often is. There may be a short projection from the posterior end of the body. In *D. glabra* the parabasal spiral usually has a maximum of 2½ turns, though *D. glabra* in *Glyptotermes* T-4538 sometimes has as many as 6, whereas in *D. parasoma* the majority of parabasals have 3 or 4 turns.

*Devescovina vestita* (fig. B, 13; pl. 5, figs. 36, 37) is much like *D. parasoma.* The mastigont structures are all similar except for the trailing flagellum, which is a stout cord. The parabasal spiral has only 2 to 2½ turns, being similar to that in *D. glabra.* The trunk of the axostyle is as stout as that of *D. parasoma,* or even stouter in its posterior part, and it projects more characteristically from the posterior end. There is a unique feature in the type of adherent rods, as is discussed in the account of the species (p. 49).

*Devescovina coghilli* resembles *D. glabra* in most respects, but there is a difference in the parabasal body that seems to necessitate taxonomic separation from it. The spiral is shorter than is usual in *D. glabra,* but its most distinctive feature is the drawn-out form (fig. B, 8), which is discussed in the account of the species (p. 43). In this characteristic there is a resemblance to the smaller forms of *Devescovina hawaiensis.* In the latter species, however, the parabasal spiral is broader, the body is appreciably broader, the cresta is wider anteriorly, and the suspensorial lamella is present.

A similarly narrow but somewhat longer cresta than that of *D. coghilli* is present in *D. uniflexura* (fig. C, 4) the parabasal of which, though also having about one turn, does not have the drawn-out spiral form. The cresta is markedly narrower than that of *D. hawaiensis,* and much longer than that of *D. exilis.* The broad loop and anterior sigmoid curve of the parabasal of *D. tendicula,* as well as the larger body size, distinguish that species from it. All other species that are comparable in other respects have more turns of the parabasal body—enough more to be of taxonomic significance in the absence of more than 1½ turns in *D. uniflexura*—except certain smaller forms of *D. glabra* from *Neotermes meruensis.* From these particular forms it can be distinguished easily by the relatively narrower, longer cresta (5μ compared to 7μ) and the narrow band-shaped instead of cordlike trailing flagellum.

## MORPHOLOGY AND DIAGNOSIS OF SPECIES OF DEVESCOVINA

### **Devescovina elongata** Bernstein

(Pl. 1, figs. 1–4; fig. B, 1)

*Devescovina elongata* Bernstein, 1928, Arch. Protistenk., 61:24, pl. 2, figs. 22–25.

*Polymastix lineata* Duboscq, Grassé, and Rose, 1937, C.r. Acad. Sci., 205:574.

*Type host.—Anacanthotermes murgabicus* Vasiljev. Turkestan.

*Additional host.—Anacanthotermes ochraceus* Burmeister. Egypt.

T-1007. Sharkiya Province. (Slides TP-1012:22; 1013:11; 1019:20; 1020:3.)

*Diagnosis.*—(From type host, after Bernstein): length 30–77μ; width 3–6μ (seldom more); four long flagella; parabasal body beginning at anterior end of nucleus, turned about once around axostyle; axostyle slender; rods present on entire surface of the body; slender bacteria often adherent by one end to entire surface. (From *Anacanthotermes ochraceus*): length 39 (22–62)μ; width 5.5 (3.5–9)μ; trailing flagellum about body length, similar in diameter to an anterior flagellum; cresta flattened thorn-shaped, length 1–2μ; parabasal turns 1 (½–2); axostyle slender, not projecting from cytosome; nucleus 4.5 (3.5–5.3)μ by 2.2 (1.7–4)μ; adherent *Fusiformis*-like organisms comparatively short and stout; stout spirochaetes, 5–9μ long, adherent over entire body surface.

I have not seen the flagellate in *Anacanthotermes murgabicus,* but the one in *Anacanthotermes ochraceus* agrees in all points described by Bernstein, and probably belongs to the same species in spite of some difference in reported size. Bernstein failed to describe the cresta, and, although she observed four flagella, she did not differentiate one as a trailing flagellum. On the basis of her description, the flagellate was not properly placed in the genus *Devescovina*—a fact noted by Duboscq and Grassé (1929, 1933). They first stated that it is *Polymastix;* later, that it is a form near *Polymastix;* and Duboscq, Grassé, and Rose (1937) proposed for it the name *Polymastix lineata.* The existence of a cresta and trailing flagellum, however, together with the coiled parabasal body and slender axostyle, place it in the genus *Devescovina.* The species shows primitive characteristics in the very small cresta, the trailing flagellum that is scarcely stouter than an anterior flagellum, and the short parabasal body.

In its typical shape the body is broadest in the anterior part and tapered posteriorly to a point. The ratio between the greatest breadth and the length is seldom as little as 1:12, as Bernstein gave it. A characteristic feature is an anterolateral indentation marking off the region of the papilla (pl. 1, fig. 2).

Bernstein gave as diagnostic of *D. elongata* the presence of two basal granules, side by side and equal in size, as in *Polymastix melolonthae* and *P. legeri* (Grassé, 1926). The blepharoplast grouping is, however, like that in other species of the genus; there seems to be a single one. Her description of the separate second granule probably is owing to observation of the proximal end of the cresta, which she misinterpreted as a granule. Her description of the origin of one of the flagella from this is in agreement with that interpretation, since one separates from the cresta.

The adherent *Fusiformis*-like microörganism (pl. 1, fig. 1) resembles "*F. legeri*" from *Polymastix legeri* more than that on other species of *Devescovina.* Its length is usually only 1 to 2μ, whereas that on other *Devescovina* species usually is 4 to 14μ, averaging about 6μ. It is even shorter than *F. legeri,* which Grassé (1926) reported varies in length from 2 to 4μ. The organism is rod-shaped, without tapering ends, as in *F. legeri,* whereas the rods on other species of *Devescovina* are relatively more slender and taper to pointed ends.

Characteristic of the species in the Egyptian host are numerous spirochaetes adherent to the surface (pl. 1, fig. 3). These are present also in the Turkestan specimens; Bernstein wrote of adherent bacteria that give the impression of a dense coat of cilia.

The cytoplasm contains numerous granules, but lacks fragments of the plant material eaten by the termites, which are often present in other flagellates of *Anacanthotermes ochraceus.* The termite feeds, not exclusively on wood, but on grass, roots, straw, and other material. The fragments in the larger Protozoa are mostly too large to be accommodated in the slender body of *D. elongata.* It is probable that, unlike other species of *Devescovina, D. elongata* is entirely saprozoic, as Bernstein indicated. Bernstein observed no wood particles, the only conspicuous cytoplasmic inclusions being highly refractive, deep-staining spherules.

### **Devescovina cometoides** de Mello and de Brito

(Pl. 1, figs. 5–11; fig. B, 2–4)

*Devescovina cometoïdes* de Mello and de Brito, 1929. C. r. Soc. Biol., 101:394. (Name mentioned only.)

*Devescovina cometoides* de Mello and de Brito, *partim,* 1929, Arqu. Esc. Méd.-Cirurg. Nova Goa, (A) fasc. 5:699, figs.

*Type host.*—*Kalotermes* (s. l) sp. Damaum, Portuguese India.

T-317. (De Mello.) (Xenosyntype slides TP-323:1, 3.)

*Additional hosts*—

*Cryptotermes dudleyi* Banks. Panama. Ceylon.
T-239. Balboa. (Homosyntype slides TP-156:4; 160:7; 161:8, 163:2.)
T-327. (Cleveland. Collier.) Paradeniya. (Homosyntype slide TP-254:1.)
*Cryptotermes* sp. Java. (Possibly = *C. dudleyi.*)
T-4572. Telawa. (Homosyntype slide TP-3235:5.)
*Cryptotermes* sp. Java.
T-329. (Cleveland. Collier.) (Homosyntype slide TP-257:4.)
*Cryptotermes* sp. nov. Madagascar. Mauritius.
T-4506. Tamatave. (Homosyntype slide TP-3190:2.)
T-4525. Reduit. (Homosyntype slide TP-3204:19, 20.)
*Cryptotermes* sp. Tanganyika Territory.
T-1013. Tanga. (Homosyntype slide TP-1024:9.)
*Glyptotermes dilatatus* (Bugnion and Popoff). Ceylon.
T-318. (Cleveland. Collier.) (Homosyntype slide TP-263:1.)
*Glyptotermes* sp. nov. Java.
T-4559, 4567, 4571. Bandjar. (Homosyntype slide TP-3229:11.)
*Kalotermes repandus* Hill. Fiji Islands.
T-516. (Hill 4064.) (Homosyntype slide TP-516:4, 2.)

*Diagnosis.*—(From type host, original): length 43 (35–58)μ; width 9.5 (6–17)μ; trailing flagellum a stout cord, not flattened; cresta length 3 (2.5–3.5)μ, anteromedial edge 1.5–2μ; parabasal coiled closely around axostyle 1–2 turns, tapering in posterior part to a blunt point; nucleus 5–6 by 2.5–3.5μ; long spirochaetes in a tuft at anterior end, and often in smaller numbers elsewhere on the entire body; *Fusiformis*-like microörganisms of long, slender type. (From *Cryptotermes dudleyi*): length 44 (29–64)μ; width 14 (11–21)μ; cresta length 3 (2.5–3.7)μ; nucleus 4.7 (4.2–5.6) by 3 (2.4–3.7)μ. (From *Glyptotermes dilatatus*): length 35 (24–48)μ; width 10.5 (7–14)μ; cresta length 3.2 (2.5–3.6)μ; nucleus 4.5 (3.8–4.8) by 2.7 (2.2–3.3)μ. (From *Kalotermes repandus*): length 49 (39–61)μ; width 15 (10–22)μ; anterior flagella 40–45μ; trailing flagellum a cord or very narrow band, not over ½μ, length 60–70μ; cresta length 3.2 (2.7–4)μ; parabasal spiral drawn out, sloping, 2 (1¾–2¾) turns, parabasal thread broad; chromatic shield present; nucleus 6.6 (5.3–8) by 3.9 (3.3–4.7)μ; spirochaetes often attached to the anterior end.

De Mello and de Brito (1929) characterized this flagellate (their species B) as long and pisciform in contrast to the stouter species (A), which I have identified with *D. lemniscata.* They reported the length as varying from 30 to 100μ, the width from 3 to 26μ. I made measurements given in the foregoing diagnosis of flagellates from the type host from slides sent by de Mello. It is probable that the excessive lengths and widths reported in the original account were based on measurements of abnormal material. The material sent by de Mello contained an unusually large number of slender forms, bringing the average width down to a lower figure than in the other hosts. This is less than is truly characteristic of the species.

It is evident in their account that de Mello and de Brito did not use valid criteria in distinguishing the two species from each other and from several already described species. They gave the cresta length as 6 to 8μ in both species, failed to observe the third anterior flagellum, described the trailing flagellum as a band in both, and made no distinction in the parabasal bodies. In examining the material, I found that the more slender forms were the same as a flagellate I had previously distinguished as a new unpublished species in *Cryptotermes dudleyi.* De Mello and de Brito doubtless considered these in their account of the species *cometoides;* but that species also included some *D. lemniscata,* as the larger cresta and ribbon trailer indicate. I have preserved their name for this species, but it must be admitted that it would be impossible to identify the form from their description alone. That is also true, however, of some other descriptions of Devescovininae. When the host is correctly identified, however, the strict specificity of flagellates of termites enables us to resolve the difficulty, even without the original preparations.

The average width of the trailing flagellum has been estimated as about a half-micron. Usually it is a cord, but in material from *K. repandus* it is often a very narrow band. De Mello and de Brito gave its length as usually between 60 and 70$\mu$, whereas the anterior flagella are 25 to 30$\mu$ long. In specimens from *K. repandus* the same length of trailing flagellum was found; the anterior flagella are longer than in their data.

The parabasal body is unlike that of *Devescovina lemniscata.* The anterior end on the anterior surface of the nuclear membrane is rounded and often enlarged. The limb passing along the nuclear membrane is comparable to the rest of the parabasal in width, but is markedly flattened. The coiling around the axostyle is close, with from one to two turns. The first turn is around the trunk of the axostyle, not around the posterior end of the nucleus as in some devescovinids with more loosely coiled parabasals. This part is broader than the parts anterior and posterior to it, and is somewhat but not very much flattened. Posteriorly, for about the length of a half-coil, the parabasal decreases in diameter and tapers to a blunt point (fig. B, 2, 3); this is unlike the situation in most devescovinids.

In certain material from *Cryptotermes* T-329 of Java, it was observed that the broadest part of the parabasal in surface view often shows a clear area in its center, thus appearing double. But since in an optical cross section an undivided, squarish block appears, it is clear that there is no actual division into two parts. In heavily stained material the parabasal body is entirely black, but on further destaining, stainable and nonstainable portions may be distinguished. The stainable portion, corresponding to the parabasal thread, is a band on the inner edge of the spiral (fig. B, 2, 3).

A chromatic shield is present in the species. It was seen most clearly in material from *K. repandus,* in which it is an elongated aggregation of granules, of definite outline and position (fig. B, 2), present in all specimens. The aggregation has in general a crestalike outline, with three edges, the apex close to, but not meeting, the blepharoplast. The granules are small and of approximately uniform size. The anterior end may extend free of the nuclear membrane. On the same slides from *K. repandus,* the chromatic shield was not evident in *D. transita.* The chromatic shield was found also in specimens from *Cryptotermes dudleyi, Glyptotermes dilatatus,* and *Cryptotermes* from Mauritius and Madagascar.

The deeply staining conical body in the anterior end of the trunk of the axostyle (pl. 1, fig. 7; pl. 2, fig. 11) is a pointed prolongation of the chromatin mass, and usually it is not detached as in *Devescovina lemniscata.* It stains with Heidenhain's and Delafield's haematoxylin like the rest of the chromatin.

### **Devescovina fissa** sp. nov.

(Pl. 2, figs. 15–21; fig. B, 5, 6)

*Type host.*—*Procryptotermes* sp. nov. Réunion.

T-4517. Pointe de Galles. (Syntype slides TP-3197: 9, 8, 4, 6.)

T-4516. Same locality. (Xenosyntype slides TP-3198:6, 8.)

*Diagnosis.*—Length 53 (39–67)μ; width 9.5 (7–14)μ; trailing flagellum a stout cord; cresta length 4.7 (4–5.5), anteromedial edge 2.5–3μ; parabasal body with narrowed longitudinal part, coiled around axostyle ¾–1¼ times, usually a little more than 1, with main part tapered posteriorly and an outgrowth coming off soon after the spiral begins, running close to the main part along the anterior edge, and often joining it again; chromatic shield of small granules present alongside of nucleus; axostyle of typical form; nucleus 5–7 by 2.5–3.5μ; entire surface bearing long, slender, adherent microörganisms; spirochaetes on anterior end only.

*Devescovina fissa* resembles *D. cometoides* more closely than any other species. The trailing flagellum is a similar stout cord. It enlarges soon after leaving the blepharoplast so that, although its maximum size is beyond the end of the cresta, it is fairly stout for most of the distance along the cresta. The cresta is larger and more elongated than that of *D. cometoides* usually is.

The parabasal apparatus is unlike that of any other species of *Devescovina* in having a branch or ramus. Some specimens lack the ramus, and the parabasal body is a simple structure enlarged at the anterior end, with a narrowed longitudinal part, spiraled about ¾–1¼ times, and tapering in the posterior part. This simple parabasal body is very much like the parabasal apparatus of *D. cometoides.* In most specimens the parabasal body has the appearance of being much broadened and split in the middle of the spiral, the two parts running transversely and being closely parallel. Of these two parts, the posterior one is the main parabasal, the anterior one is the outgrowth. The outgrowth comes off from the other part about a half-turn after the spiral begins (fig. B, 5), runs parallel for a distance of a half-turn of the spiral or less, and then either ends independently (fig. B, 6) or, more frequently, seems to be fused to the other part (pl. 2, figs. 17, 18). It is usually somewhat more slender than the main part (pl. 2, figs. 15, 16). Transitional stages in development of the ramus of the parabasal from a bud to its full size were found in Schaudinn-Delafield material.

In Delafield-stained material the narrow cleft is clear. In Flemming-Regaud material the cleft is less conspicuous, and if such preparations alone were examined it might be supposed that the parabasal was merely much broadened and tended to become double. The chromophile substance is not a filament, but a broad band occupying the full width of the inner edge, and is fairly thick.

The chromatic shield (pl. 2, figs. 20, 21) may readily be observed in suitably stained material. Well-differentiated Schaudinn–iron-haematoxylin material is best. It is a group of small, deep-staining granules extending from the blepharoplast to near the posterior end of the nucleus.

The entire surface is striated by long, slender microörganisms of the type that occurs on most species of *Devescovina.* Moderately long spirochaetes occur in a group on the anterior end of the body, but are not present elsewhere, whereas in *D. cometoides* spirochaetes are usually present in abundance on the middle and posterior parts of the body as well.

### **Devescovina tendicula** sp. nov.

(Pl. 3, figs. 22–24; fig. B, 7; fig. D, 5)

*Type host.*—*Kalotermes jeannelanus* Sjöstedt. East Africa.

T-1064. Moshi, Tanganyika Territory. (Syntype slide TP-1056:1.)
T-2013. Mount Meru, T. T. (Xenosyntype slides TP-1083:2, 12.)
T-1092. Taveta, Kenya Colony.
T-3015. Ruindi River, near Rutshuru, Belgian Congo. (Xenosyntype slide TP-2033:22.)
T-3023. Mbarara, Uganda.
T-3024. Muhoroni, Kenya. (Xenosyntype slides TP-2041:16, 26.)
T-3049. Near Iringa, T. T. (Xenosyntype slide TP-2053:1.)
T-2087, 2088. Hoima, Uganda. (Xenosyntype slide TP-2027:3.)

*Diagnosis.*—Length 56 (43–71)μ; width 16 (12–21)μ; trailing flagellum a moderately stout cord; cresta length 7 (5–8)μ, anteromedial edge 2–2.5μ; parabasal body with a sigmoid curve in the longitudinal part, turned widely about once around posterior part of nucleus; chromatic shield present; axostyle of usual form; nucleus 5–9 by 3.5–5.8μ, surface bearing long, slender, longitudinally adherent microörganisms; spirochaetes, many of which measure 15μ or more, densely cover the anterior part of the body from the parabasal loop forward.

The blepharoplast is a single granule into which one root of the anterior flagella passes directly, without enlargement. The other root ends at an enlargement or granule (pl. 3, fig. 22) smaller than the blepharoplast, close to it and connected with it by a fine fibril. The trailing flagellum is a cord, not flattened, and more slender than the trailing flagellum of *Devescovina cometoides.*

On certain slides the cresta was shorter than on others; that was true of TP-1056. On many other slides the minimum length was about 6μ, but on slides of that series the length ranged from 5 to 7μ. These specimens were also somewhat smaller in general size and in nuclear size, increasing the range of the latter.

The most noticeably unique feature of the species is the parabasal body. Posteriorly there is about one turn around the posterior part of the nucleus; not, as in most species, around the trunk of the axostyle. The posterior end of the parabasal is usually very close to the beginning of the turn, though shifted a little posteriorly, so that the parabasal forms almost a circle. The posterior part tapers to an end that is usually bluntly pointed, sometimes sharply pointed.

The longitudinal part of the parabasal has a constant, curved form (fig. B, 7). The part near the blepharoplast is straight. Instead of continuing straight to the transverse bend, as in most species, it curves from about the middle so that, with the first part of the loop, the shape is that of an inverted question mark. The stem of the question mark enlarges toward the blepharoplast, and the end is broad. The structure in the first part of the curve is considerably narrower than in the parts anterior and posterior to it.

The anterior end of the parabasal is close to the blepharoplast; it does not

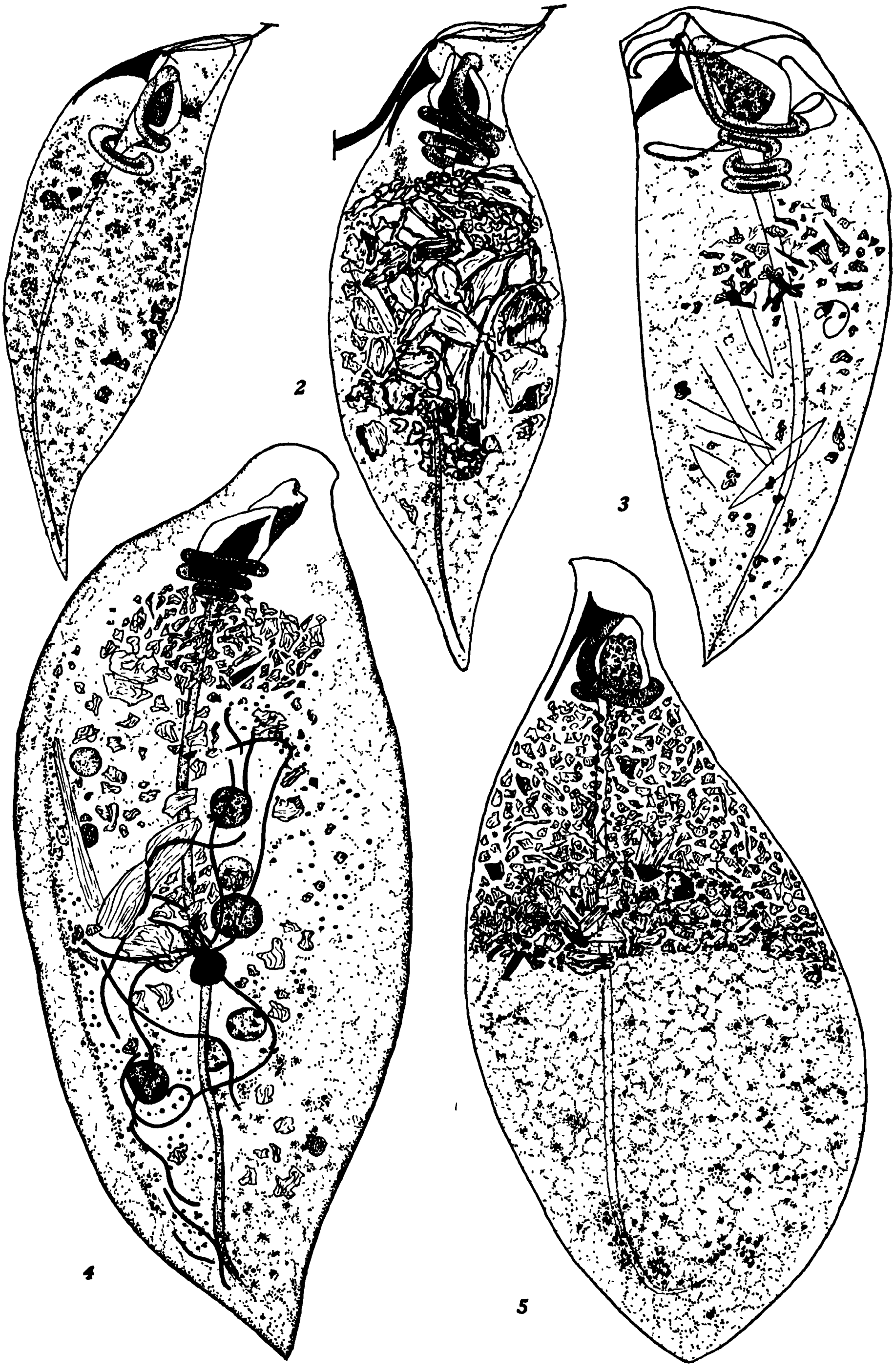

Fig. D. Wood and certain other cytoplasmic inclusions in *Devescovina*. × 1700. 1, 2. *Devescovina hawaiensis* from *Neotermes connexus*. Specimens on the same slide, 1 with almost no wood particles, 2 with much wood. 3. *Devescovina insolita* from *Kalotermes* (s.l.) sp. T-4240. Moderate amount of wood generally distributed in cytosome; also some clear spindle-shaped bodies. 4. *D. vittata* from *Kalotermes* (s. str.) sp. nov. T-3025. Wood generally distributed, and spirochaetes in cytoplasm; aggregate of small wood particles just posterior to the parabasal body. 5. *D. tendicula* from *Kalotermes jeannelanus*. Wood particles restricted to the anterior part of the cytosome, giving two distinct regions.

continue in a hook or bend beyond this point, as in many devescovinids. On the inner side of the curve is a chromophile band (pl. 3, figs. 23, 24), which appears thicker in certain Flemming-fixed material than in Schaudinn-fixed material. It continues as a filament along the edge of the sigmoid curve and is stout enough to be very distinct up to a short distance from the anterior end. Then it is reduced to a fine filament, separates from the other substance, and passes near the anteromedial edge of the cresta to the blepharoplast (pl. 3, fig. 23). This species differs from some others in the close approximation of the chromophile element to the other substance until almost the anterior end.

The chromatic shield of small granules (pl. 3, fig. 24) has a shape in optical section very much like the cresta. It is much like the chromatic shield of *Caduceia theobromae* of the same host (Kirby, 1938*a*, p. 8).

In many specimens fixed in Flemming's solution the chromatic mass consisting of small and large deep-staining granules fills up all the space within the membrane. At a variable position is the peripheral, spherical nucleolus surrounded by a sharply defined clear space. The clear space between the membrane and the chromatic mass is more or less well marked in Schaudinn-fixed material.

The axostyle tapers to a filament within the cytoplasm and is sinuous in its posterior part (pl. 3, fig. 22).

Characteristic of *Devescovina tendicula* is an unusual feature in the distribution of intracytoplasmic materials. There are two distinct regions (fig. D, 5): an anterior region amounting to about a third or half of the postnuclear portion of the body, and a posterior region. The anterior region usually contains numerous small particles of wood. Wood particles may also be present in the other region, but in almost all specimens on certain slides they have accumulated anteriorly, near the nucleus and successively posteriorly from that. In some specimens the wood particles are few or absent. Nevertheless, the cytoplasm of the anterior region is different in appearance from the rest. It has a coarsely alveolar appearance, and is clearer. The cytoplasm of the posterior region is much more finely alveolar and contains numerous granules of a type that is absent from the anterior region; in stained material, consequently, this part of the body is darker.

In *Caduceia theobromae* there is an even distribution of materials in the cytoplasm posterior to the nucleus, except for the absence of wood from the peripheral zone.

The distribution of surface organisms corresponds more or less to the limits of the two regions of the cytosome. *Fusiformis*-like rods are present on the posterior part, but are absent from the anterior part, often a third or half of the body. These rods are of the type usual on *Devescovina*, and are longer and somewhat slenderer than the rods on the limited area at the posterior end of *Caduceia theobromae.*

Spirochaetes, many of which have a length of 6 to 9$\mu$, are present on the anterior part of the body. They are particularly numerous on the anterior end. Elsewhere, although abundant, they are much more sparsely distributed than the spirochaetes on *Caduceia theobromae,* which seem on the average to be shorter. On *D. tendicula,* among the smaller spirochaetes there are some larger ones reaching 25$\mu$ in length. These vary in abundance and distribution, being numerous on some specimens and absent from others.

### **Devescovina glabra** Grassi

(Pl. 2, figs. 12–14; fig. B, 9, 10; fig. E, 2–4)

*Devescovina glabra* Grassi, 1917, Mem. R. Accad. Lincei, (5) 12:54, pl. 9, figs. 18–27.

*Type host.*—*Cryptotermes havilandi* Sjöstedt. Nigeria.
T-319. (Silvestri.) (Xenosyntype slide TP-324:1.)

*Additional hosts*—
*Cryptotermes* sp. Tanganyika Territory.
T-1034, 1035*a*. Amani. (Homosyntype slides TP-1037*a*: 1, 5; 1038:6.)
*Cryptotermes* sp. T. T.
T-1035*b*, 1041. Amani. (Homosyntype slides TP-1037*b*: 8; 1046:1.)
*Cryptotermes* sp. Kenya Colony.
T-1091. Taveta Forest. (Homosyntype slide TP-1079:4.)
*Cryptotermes* sp. Zanzibar.
T-3092. (Homosyntype slide TP-2064:8.)
*Cryptotermes* sp. Portuguese East Africa, South Africa.
T-4003. Beira. (Homosyntype slides TP-2066:7, 9, 19.)
T-4260. Near Bremersdorp, Swaziland. (Homosyntype slide TP-3077:9.)
*Cryptotermes* sp. nov. Madagascar.
T-4403. Near Tulear. (Homosyntype slide TP-3151:13.)
T-4469. Near Ambovombe
*Cryptotermes* sp. Madagascar.
T-4303. Near Maevatanana. (Homosyntype slide TP-3095:11.)
T-4361, 4375. Near Mahabo.
*Cryptotermes* sp. Java. (Det. as *Cr. dudleyi* by Emerson.)
T-4556.Telawa. (Homosyntype slide TP-3234:23.)
*Glyptotermes caudomunitis* Kemner. Java.
T-4566. Bandjar. (Homosyntype slide TP-3242:17.)
*Glyptotermes* sp. nov. Sumatra.
T-4538. Kateman. (Homosyntype slides TP-3219:18, 14, 3.)
T-4562. Same locality.
*Kalotermes* (s. str.) sp. Madagascar.
T-4341. Near Maevatanana. (Homosyntype slide TP-3106:11.)
*Neotermes zuluensis* Holmgren. South Africa.
T-4249. Warmbaths, Transvaal. (Homosyntype slide TP-3071:6.)
T-4267. Near Bremersdorp, Swaziland. (Homosyntype slide TP-3080:7.)
T-4276. Nsoka, Transvaal. (Homosyntype slides TP-3083:1, 2; 3091:9.)
*Neotermes meruensis* Sjöstedt. East Africa.
T-1080,1081,1093. Taveta, Kenya Colony. (Homosyntype slides TP-1067:4; 1075:2.)
T-2009. Near Arusha. Tanganyika. (Homosyntype slide TP-1081:4.)
T-2040–2042, 2044–2048. Embu, Kenya Colony. (Homosyntype slides TP-2010:9, 23, 25; 2008:11.)
T-2049. Meru, Kenya Colony. (Homosyntype slide TP-2009:6.)
T-3026. Near Ngorongoro Crater. (Homosyntype slide TP-2046:13.)
T-3048, 3055. Southern Tanganyika. (Homosyntype slide TP-2051:5.)
*Neotermes* sp. nov. Madagascar.
T-4358. Near Malaimbandy. (Homosyntype slide TP-3122:14.)
T-4373. Near Mahabo. (Homosyntype slide TP-3140:20.)

**_Diagnosis._—(From type host, original): length 44 (27–58)$\mu$; width 15 (11–20)$\mu$; trailing flagellum very narrow, band-shaped or cord-shaped; cresta length 7 (6–8)$\mu$; parabasal body turned 1½–3 times, usually 2 or more, longitudinal part flattened, often enlarged at anterior**

end; nucleus 5.5 (5–6) by 4.4 (3.5–4.5)μ; long, slender rods adherent longitudinally to surface of body; no adherent spirochaetes. (From *Neotermes meruensis* T-2045): length 38 (24–47)μ; width 9.5 (7.5–12.5)μ; anterior flagella 35–45μ; trailing flagellum a stout cord, 60–65μ; cresta 5 (4.5–5.5)μ, anteromedial edge about 2μ; parabasal turns 1⅕ (⅞–1½), nucleus 4.5 (4–5) by 3 (2.5–4)μ; aggregation of granules posterior to nucleus; no spirochaetes. (From *Neotermes meruensis* T-1080): besides the smaller forms as described above, larger forms are present, viz., length 55 (42–68)μ; width 17 (15–22)μ; cresta 6 (5.5–7)μ; parabasal turns 1½ (¾–2½); nucleus 6.2 (5.8–6.6) by 4.2 (3.3–4.9)μ. (From *Kalotermes* T-2009): chromatic shield present; thick tuft of long spirochaetes adherent to anterior end. (From *Kalotermes* T-4276): length 39 (27–48)μ; width 15.5 (10–20)μ; trailing flagellum a stout cord; cresta 5.5–7μ, anteromedial edge 2–2.5μ; parabasal turns 1¾ (1–2½); nucleus 5.8 (5.1–6.8) by 4.3 (3.4–5.1)μ; aggregation of granules or rods posterior to nucleus; group of spirochaetes adherent to anterior end. (From *Cryptotermes* T-4003): length 53 (38–66)μ; width 12 (8–15.5)μ; trailing flagellum a very narrow band; cresta 7.5 (6.6–8.8)μ; parabasal turns 1½ (1–2); nucleus 5.2 (4.1–5.8) by 3.5 (3.3–4.1)μ; aggregation of granules not well developed. (From *Cryptotermes* T-1035*b*): cresta short; body surface covered with adherent spirochaetes, and a tuft on the anterior end. (From *Cryptotermes* T-1041): cresta longer; trailing flagellum a narrow band. (From *Glyptotermes* T-4538): length 49 (39–65)μ; width 15 (10–17)μ; cresta 5 (4.5–5.5)μ, anteromedial edge about 2μ; parabasal body spiraled 1¾–6 times; nucleus 5–7 by 4–6μ.

Grassi's name *glabra* seems to have been based on the supposed absence of surface microörganisms. Bernstein (1928) assumed that Grassi meant that "pellicular striations" were absent. Grassi did not so state in his text, but no striations are shown in his figures. It is more likely, however, that he had reference to the absence of "immobile cilia" (spirochaetes) like those he had just described on *Devescovina* (=*Metadevescovina*) *stereociliata*. *Fusiformis*-like microörganisms ("pellicular striations") are present on *D. glabra* as on all other species of *Devescovina.*

Grassi's description is brief and very inadequate; it discusses none of the taxonomic characteristics necessary to distinguish species of *Devescovina* from one another. The figures, however, are detailed and accurate, although one (fig. 18) shows the parabasal body spiraled in the wrong direction. In addition to those figures, I have had reference, through the kindness of Professor Silvestri, to a slide made from *Cryptotermes havilandi.*

The specimens assigned to *Devescovina glabra* show certain minor differences in different hosts, but these have not seemed sufficient to split off separate species.

The trailing flagellum is a very narrow band in the majority of specimens from the type host, though in many it is a cord. In *D. glabra* from *Neotermes meruensis* this flagellum is a stout cord. That is true also of the other material from African termites, except *Cryptotermes* T-4003, in which it is a narrow band as in the type. In specimens from *Cryptotermes* T-4260 the band form is still more marked. In the Madagascar hosts the flagellum was observed to be a cord or a band in different flagellates from the same termites. Clearly, there is no significance in a small difference in this characteristic.

The blepharoplast is a compact group of several granules; from it a short rhizoplast extends to the nuclear membrane. The cresta is of a uniform type in all the variants of *D. glabra,* though there is some variation in length. The smallest crestas, in *Neotermes meruensis* T-2045, with a length of 4.5 to 5.5μ, ranged below the minimum usual in most other material; but others were comparatively uniform in length. The anteromedial edge, at 2 to 2.5$\mu$, is relatively short, and the cresta does not flare anteriorly as much as in some species (*D. hawaiensis,* for example). It is not, however, so straight sided as is shown in Grassi's figures.

The parabasal turns vary in different material. In the specimens on the type slide there were more than in most others, exceeding the usual condition in the species. Successive turns around the trunk of the axostyle are often quite close together, often separated by the width of the parabasal or more. The longitudinal part is narrower than elsewhere, and the anterior end is variable. Sometimes the parabasal ends close to the blepharoplast without enlargement, but usually there is a more or less prominent enlargement, and often, particularly in larger specimens, the parabasal is extended in a short hook on the anterior surface of the nucleus.

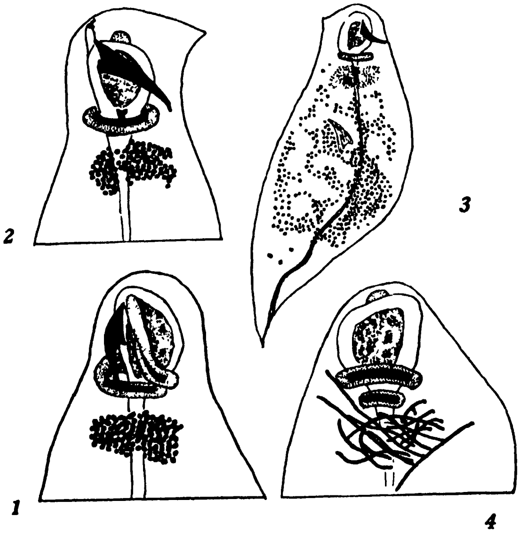

Fig. E. 1. *Devescovina lemniscata* from *Neotermes castaneiceps.* Aggregate of granules in a ring around the axostyle, present in most specimens of this material. × 1700. 2, 3. *D. glabra* from *Neotermes meruensis;* 2, aggregate of granules (bacteria) characteristic of this material, × 2330; 3, bacteria in cytoplasm of a large percentage of the specimens, showing also the position of the ring. × 1150. 4. *D. glabra* from *Neotermes zuluensis;* long rods in place of the granules. × 2330.

The chromophile element appears as a band in well-stained material, and a filament in much differentiated material. It borders the longitudinal part to close to the end of the anteromedial edge of the cresta, where it separates and passes directly to the blepharoplast.

The chromatic shield was readily observed in certain material from *Neotermes meruensis* T-2009, but search did not reveal it in material from other hosts. Probably, however, it is present in all.

The anterior part of the trunk of the axostyle is stout, and is straight or smoothly curved. The posterior quarter or so is a filament, often sinuous, extended into the pointed end of the body (pl. 2, fig. 12) or recurved in the cytoplasm.

Characteristic of this species is a grouping of deep-staining granules or rods around the trunk of the axostyle a short distance posterior to the parabasal body (fig. B, 10; fig. E, 2, 3). Grassi's figures 19 and 27 show a group of granules in the position usual in the material of *D. glabra* observed by the writer in other hosts. The slide from the type host was not adequately prepared to show this group of granules, but there was some indication of its presence. In material from *N. meruensis* and other hosts it was conspicuous.

The position and form of the aggregation in *D. glabra* from *Neotermes meruensis* is constant, and it has been found in all specimens from several colonies of termites. In most specimens the limits of the aggregate are well defined; in some, however, the granules are more scattered, so that the outlines are more diffuse, or (in a few) they are so much scattered that no aggregate is to be recognized. The aggregate usually has the form of a thick ring around the axostyle, beginning at a distance of 1 to 2μ posterior to the nucleus. The outside dimensions of the ring are often about 1.5–3 by 3.5–5μ. The granules are of moderate size and resemble some that are scattered throughout the cytoplasm. They stain deeply with both Delafield and Heidenhain haematoxylin, after all fixatives used.

Similar aggregations, with some variations in form and abundance, were rather uniformly present in other material of *Devescovina glabra.* In many specimens on a slide from *Neotermes zuluensis* the usual short rods or granules were replaced by relatively long rods (fig. E, 4). Probably this is a symbiotic microörganism.

In some material larger granules are also present (fig. E, 3), scattered in the cytoplasm and sometimes very abundant. These probably are another kind of symbiotic microörganism, which is present only occasionally.

The *Fusiformis*-like rods are of the long, slender type. No spirochaetes are regularly adherent to *D. glabra* in most hosts, but there are exceptions. In T-2009, T-3026, and T-4276 numerous stout spirochaetes, many of them 10–15μ long, adhered to the anterior end of all specimens observed. Spirochaetes were present in abundance on the entire surface of many specimens of *D. glabra* from *Cryptotermes* T-1035*b* from Amani. In this host it is associated with a large species of *Foaina.* In *Cryptotermes* T-1035*a,* collected also at Amani in the same series of smears, this species of *Foaina* is absent and spirochaetes are lacking entirely from *D. glabra.* A short cresta and an investment of spirochaetes occur also in specimens from *Cryptotermes* T-3092 from Zanzibar. *Cryptotermes* T-1041 from Amani, which is probably the same species as T-1035*b,* has a more typical *D. glabra,* with a longer cresta and a narrow band-shaped trailing flagellum. In view of this, and the variation in cresta length in specimens from *Neotermes meruensis,* it does not seem possible to establish a separate species for these forms. Nevertheless, the arrangement is not entirely satisfactory, as there are marked differences from the specimens in the type host.

### **Devescovina coghilli** sp. nov.

(Fig. B, 8)

*Type host.*—*Cryptotermes merwei* Fuller. South Africa.
T-4012. Durban, Natal.
T-4048. Port Shepstone, Natal. (Syntype slides TP-2088:3, 14; 2093:6.)
T-4088. Zuurberg Pass, Cape Province.
T-4109. Wilderness, Cape Province.
T-4114. Near Knysna, Cape Province.

*Diagnosis.*—Length 39 (30–49)μ; width 7.5 (6.5–9)μ; trailing flagellum a moderately stout cord; cresta length 5.5–6.5μ, anteromedial edge about 1.5–2μ parabasal body turned 1–1½ times, usually about 1, in a drawn-out spiral; chromatic shield present; nucleus with no space between membrane and chromatic mass, 4.5 (4.1–5) by 2.9 (2.5–3.3)μ; surface bearing long, slender, longitudinally adherent microörganisms; spirochaetes about 10μ long adherent to the anterior end.

The blepharoplast is a single, fairly large body evidently composed of several granules, with no separate granule or enlargement on one of the flagellar roots. On several specimens the anterior flagella ranged in length from 40 to 45μ, the trailing flagellum from 54 to 60μ.

In cresta and trailing flagellum the flagellate resembles *Devescovina glabra,* but the parabasal body is different enough to justify specific separation. Generally there is only one turn, sometimes a little more. The spiral slopes markedly, so that the end of the turn is situated a certain distance posterior to the beginning (fig. B, 8). In *D. glabra,* the parabasal of which generally has more turns, the first turn is more horizontal, so that the end is close to the beginning.

The chromophile element of the parabasal body is a band in the first part of the spiral, and tapers posteriorly. It separates as a deep-staining filament in the posterior part of the longitudinal portion and passes straight to the blepharoplast.

In a large proportion of specimens the other substance of the parabasal is enlarged at the anterior end, but does not turn in a hook of any length. Some specimens have a short part beyond the point closest the blepharoplast.

The nucleus is different from that of most species of *Devescovina* in that in no specimens, however fixed, was any space observed between the nuclear membrane and the chromatin mass. The space was evident in both Schaudinn-fixed and Flemming-fixed specimens of *D. glabra.* The chromatin is in discrete, dispersed granules, not so compact a mass as in most species of *Devescovina.* Peripherally placed at a variable position is a nucleolus in a clear area. Several nuclei of *D. coghilli* parasitized by *Nucleophaga* have been seen. In these the granules are often larger, more evenly distributed, and the nucleus is hypertrophied. In the normal nucleus, however, there is some suggestion of the appearance of the parasitized nucleus.

There is no aggregation of granules or rods posterior to the nucleus as in *D. glabra,* and no accumulation of wood particles in that region as in *D. tendicula.* The intracytoplasmic materials are evenly distributed.

The *Fusiformis*-like microörganisms are the same in morphology and arrangement as those on most species of *Devescovina.*

### **Devescovina insolita** sp. nov.

(Pl. 3, figs. 26, 27; fig. B, 12; fig. D, 3; fig. F)

*Type host.*—*Neotermes* sp. Tanganyika Territory.

T-2012. Mount Meru. (Syntype slides TP-1082:18, 11, 20.)

*Additional host.*—*Kalotermes* (s.l.) sp. Transvaal, South Africa.

T-4240. Near Nylstroom. (Homosyntype slides TP-3069:10, 11.)

*Diagnosis.*—Length 54 (47–64)μ; width 17 (11–22)μ; trailing flagellum a moderate cord; cresta broad, length 5.5–7μ, anteromedial edge 3–3.5μ, posteromedial edge 4.5–6μ; parabasal body with 1–3 turns, usually 1½–2½; capitulum of axostyle broadly expanded anteriorly and dorsally, prolonged in a tapering membrane passing transversely or obliquely on the left side of the nucleus to the opposite edge of the body; trunk of axostyle filamentous posteriorly; nucleus 7–8 by 4.5–6μ; granules present on one side of the trunk of the axostyle inside the parabasal and on the adjoining parts of the nuclear membrane, possibly symbionts; anterior third to half of the body free of adherent rods; spirochaetes, many about 10μ long, present on anterior end, few elsewhere.

The blepharoplast group is small, compact, and composed of several granules. The anterior flagella pass along the papilla as two roots, both stouter than the free parts of the flagella. These roots, running parallel, extend as relatively stout fibers, about equal in thickness to a short distance from the blepharoplast. Each is connected to the blepharoplast by a fine fibril (fig. F, 1).

A short, straight rod passes from the part of the blepharoplast to which the cresta and trailing flagella connect, and extends into the region between the cresta and the roots of the anterior flagella. It is a constant and well-defined structure in this flagellate.

The anterior end of the parabasal body is close to the blepharoplast, with no hooklike extension beyond it as in many devescovinids (pl. 3, fig. 27). The anterior end is enlarged a little, but much less than in some other species. The anterior part of the parabasal body passes obliquely across the nucleus, beginning near one side anteriorly and passing near the other side posteriorly. The posterior part is wound rather closely around the trunk of the axostyle, and the posterior end is rounded with no diminution in diameter. A slender parabasal thread at the inner edge of the spiral is well defined in iron-haematoxylin preparations.

The capitulum of the axostyle is complex, and more like that in certain species of *Metadevescovina* than that in other species of *Devescovina.* After spreading out between one side of the nucleus and the anterior part of the parabasal body, and ventral to this region, it passes in a broad membrane near the anterior edge of the body. In its posterodorsal part the capitulum is prolonged in a tapering membrane which passes transversely or obliquely on the left side of the nucleus, with its pointed end at the dorsal periphery of the body (pl. 3, fig. 27). The anterior edge of this membrane appears as a well-defined filament in iron-haematoxylin preparations (pl. 3, fig. 26). Optically, edges elsewhere appear as filaments. The interpretation as a capitular membrane is based largely on the appearance of these filaments in differently oriented specimens, as well as on an occasional recognition of a membranous structure, and on comparison with other devescovinids.

The trunk of the axostyle is stout for the greater part of its length, but becomes reduced to a filamentous end usually entirely enclosed within the cytoplasm, as in most species of *Devescovina.* In many normal specimens the slender posterior end of the axostyle projects for a few microns from the pointed end of the body.

Characteristic of the species is the presence of a group of granules against one side of the trunk of the axostyle, within the spiral of the parabasal body, and against parts of the nuclear membrane (fig. B, 12). The number of these granules varies, but some at least were present in all specimens observed. Similar granules are also sometimes present along the inner side of the proximal part of the posterior membranous extension of the capitulum. In one specimen, similar granules were extended beyond their usual region of distribution in the cytoplasm of the anterior part of the body and were present in irregular masses posterior to the parabasal body (fig. F, 2).

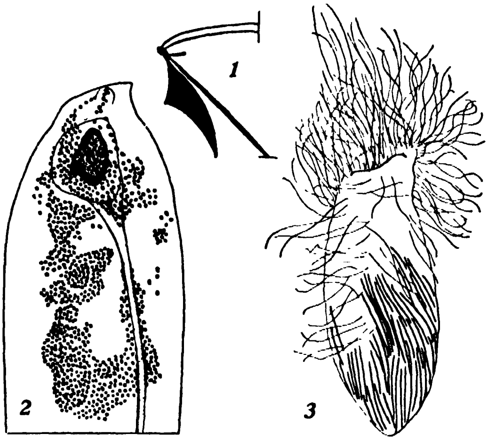

Fig. F. *Devescovina insolita* sp. nov. from *Neotermes* sp. 1. Diagram showing cresta, blepharoplast group, attachment of the two roots of the three anterior flagella and the trailing flagellum, and the rod extending from the blepharoplast. × 1800. 2. Granules in cytoplasm around and posterior to nucleus, probably symbionts. × 1275. 3. Rod-shaped bacteria adherent to the posterior part of the body, spirochaetes on anterior part and elsewhere. × 680.

Long, slender surface rods are present, as is usual in *Devescovina,* but on the posterior part of the body only. They are entirely lacking from the anterior third or half (fig. F, 3).

A dense tuft of spirochaetes is characteristically present on the anterior end, but some specimens lack it. The area covered by the spirochaetes is not so sharply restricted as in some species. Similar spirochaetes may be scattered elsewhere on the surface, but there is no dense tuft on the posterior end.

### **Devescovina robusta** sp. nov.

(Pl. 3, fig. 25; fig. B, 11)

*Type host.—Neotermes erythraeus* Silvestri. Eritrea.

T-312. (Silvestri.) (Syntype slides TP-321:1, 2.)

*Diagnosis.*—Length 54 (38–69)μ; width 22 (14–29)μ; trailing flagellum a cord of moderate thickness; cresta length 6.4 (5–8.3)μ, anteromedial edge 1–1.5μ; parabasal body turned loosely 1½–2½ times, last part often extended out straight; trunk of axostyle stout, not filamentous posteriorly; nucleus 9 (7.5–10.5)μ by 6 (4.5–7.5)μ; rodlike microörganisms present only on the posterior half to quarter of the body, elsewhere some short adherent spirochaetes.

This species is larger in size and has a larger nucleus than most other species of *Devescovina.* It occurs in the same host as *Caduceia nova* (Grassi), but Grassi did not describe it. I mentioned (1936) its presence there, in connection with an account of *Caduceia nova.*

The two devescovinids have certain resemblances. The adherent microörganisms are of the same type; and the *Fusiformis*-like form is restricted to the posterior part of the body in *D. robusta* and occurs in an area at the posterior end of *C. nova.* Similar rods are often present in the cytoplasm of both species. Short spirochaetes adherent to the surface of the body not covered by *Fusiformis* are present in both.

The axostyles are similar in the two devescovinids, and that of *D. robusta* differs from the type usual in the genus in being stouter and not filamentous in its posterior part (pl. 3, fig. 25). The nuclei are also much alike, and the crestas are of similar shape.

The size is markedly different, *Caduceia nova* averaging 88μ long (64–138), *D. robusta* 54μ (38–69). Although the range overlaps, distribution curves are separate; only a very few *D. robusta* are so long as 64μ, and very few *C. nova* are so short. Apart from exceptional specimens, there is no intergradation in size as a whole or in that of individual organelles, such as cresta or nucleus.

The two devescovinids differ notably in the parabasal apparatus, and there is no intergradation in its form. The proximal element in *C. nova* is turned first in a wide loop around the axostyle posterior to the nucleus, then in a long loose spiral drawn out along the trunk of the axostyle; from one to six cords are attached to this element (Kirby, 1936, pl. 16). The parabasal of *D. robusta* is coiled in the usual *Devescovina* manner, though loosely, and there are no rami (fig. B, 11).

Only two slides sent by Silvestri have been available for study of this flagellate. To establish the relationship, if any, to *Caduceia nova,* of which, except for the parabasal apparatus, it is a miniature, more material is desirable. Additional evidence for the separateness of the two is adduced from the fact that *Caduceia nova* occurs also in *Neotermes* sp. T-2012 from Tanganyika, but there is no flagellate like *D. robusta* in that termite. Instead, there is the unique *D. insolita. D. insolita* is present also in *Kalotermes* T-4240 from the Transvaal, but in that host it is accompanied not by *C. nova,* but by *C. theobromae.*

### **Devescovina parasoma** sp. nov.

(Pl. 3, fig. 29; pl. 4, figs. 30–32; fig. B. 14)

*Type host.—Neotermes tectonae* (Dammerman.) Java, Sumatra.
T-311. Djember, Java. (Cleveland. Collier.) (Syntype slide TP-251:5.)
T-4561. Kateman, Sumatra. (Xenosyntype slide TP-3221:3.)

*Additional hosts*—

*Neotermes dalbergiae* Kalshoven. Java.
T-4568. Bandjar. (Homosyntype slide TP-3231:8.)
*Neotermes sonneratiae* Kemner. Java.
T-4575. Angke. (Homosyntype slide TP-3253:4.)
*Cryptotermes* sp. nov. Java.
T-4553. Tapos. (Homosyntype slide TP-3237:1.)
*Cryptotermes* sp. Java. (Det. as *C. cynocephalus* Light by Emerson.)
T-4582. Buitenzorg. (Homosyntype slide TP-3250:2.)
*Cryptotermes* sp. Kenya Colony.
T-1086. Taveta. (Homosyntype TP-1060:5.)

*Diagnosis.*—(From type host): length 43 (24–60)μ; width 19 (11–27)μ; trailing flagellum a very narrow ribbon; cresta length 5.2 (4.4–6)μ, anteromedial edge 2–2.5μ; parabasal body coiled tightly 1½–4 times, 3–4 in majority; coil of decreasing diameter; chromatic shield present; posterior part of trunk of axostyle stouter than is usual in the genus, often projecting a few microns; nucleus 5.6 (4.4–6.2) by 4.6 (3.6–5.3)μ; *Fusiformis*-like rods adherent to surface, often irregularly arranged; spirochaetes 8–14μ long adherent over whole body surface of most individuals; stout, rod-shaped microörganisms 3–12μ long often adherent to posterior end. (From *Neotermes dalbergiae*): length 32 (25–42)μ; width 12 (9–19)μ; nucleus 4.3 (3.3–6.1) by 3.6 (2.6–4.5)μ; cresta length 5.1 (4.4–5.5)μ. (From *Cryptotermes* T-1086): cresta length 4–5μ; body surface covered with adherent spirochaetes, except the anterior end.

In thirty of fifty specimens from *Neotermes tectonae* the parabasal body had from three to four turns. Adjacent turns are very close together, and the diameter of the spiral diminishes posteriorly; that of the last of four turns may be only half that of the first (pl. 4, fig. 32).

The chromophile element appears as a rather thick band the full width of the inner edge of the spiral in Champy- and Flemming-fixed material that is not too much destained. The greater the degree of extraction, however, the smaller the chromophile element appears; and in certain Schaudinn- and Hollande-fixed material it is only a stout filament.

The longitudinal portion of the parabasal is somewhat smaller in diameter than the spiraled portion, and the chromophile element is a filament along its nuclear edge. The filament does not separate until near the anterior end of the cresta, where, instead of turning on the nuclear membrane with the other substance, it passes over one side of the parabasal directly to the blepharoplast.

The other substance usually ends near the blepharoplast, but in many larger specimens there is an extension beyond this point. The anterior end of the parabasal is usually enlarged little or none at all, in contrast to the situation in some devescovinids.

The trunk of the axostyle (pl. 4, fig. 32) is stouter in its posterior portion than in most species of the genus, resembling the axostyles of *D. robusta* and *D. vestita*. It is not sinuous, but extends through the body straight or in a smooth curve, and often projects a few microns beyond the posterior end. A chromophile band appears in some material just anterior to the point of exit from the body.

In some material the nucleus showed no space under the membrane (pl. 3, fig. 29; pl. 4, fig. 31); in other material a clear space of variable width was present (pl. 4, fig. 32).

The microörganisms adherent to the surface of *Devescovina parasoma* from *N. tectonae* and *N. dalbergiae* (pl. 4, fig. 30) are of three kinds. (1) Long, slender rods adherent by their full length in a more or less longitudinal direction are universally present. They vary in length and direction, and tend to be aggregated in groups. (2) Long spirochaetes adherent by one end are distributed over the entire surface. The presence of these is characteristic of the species. Although they occur on most individuals, their number varies and they are absent from some specimens, both in *Neotermes tectonae* and, more frequently, in *Neotermes dalbergiae*. (3) In many specimens rod-shaped organisms are adherent in small numbers, usually on the posterior portion of the body. They vary in length from about 3μ to 12μ; the larger ones are curved or somewhat spiraled. There is a linear differentiation of alternating stained and unstained material in Schaudinn-iron haematoxylin material. Many of the rods are free in the gut contents, but a large number are adherent to the body of *Devescovina parasoma*.

### **Devescovina vestita** sp. nov.

(Pl. 4, figs. 33–35; pl. 5, figs. 36–38; fig. B, 13)

*Type host.*—*Glyptotermes niger* Kemner. Java.

T-4543. Tapos. (Syntype slides TP-3218:20, 18, 10, 3.)

T-4545. Tapos. (Xenosyntype slide TP-3254:4.)

*Diagnosis.*—Length 45 (37–54)μ; width 16 (12–19)μ; trailing flagellum a stout cord, not flattened; cresta length 4.9 (4.5–5.5)μ, anteromedial edge 2.5–3μ, posterior part narrow; parabasal body spiraled closely around axostyle 2–2.5 times, usually about 2; chromatic shield present; trunk of axostyle straight or smoothly curved, not sinuous, not tapering to filament in cytoplasm, projecting for a distance up to 10μ; nucleus 5.7 (5–6.6) by 4.1 (3.3–5)μ; rods adherent to the surface shorter (often 4–6μ), stouter, and more irregular in alignment than in most other species of *Devescovina;* spirochaetes, often 10μ long, abundant on the entire surface posterior to the nucleus.

The longitudinal part of the parabasal body is somewhat, but not very much, narrowed in the middle. At the anterior end it enlarges a little. It turns away from the blepharoplast for only a short distance. Successive turns of the parabasal are usually close together (pl. 4, figs. 33, 34); the space may be very narrow, or they may be in actual contact. The spiral is wound fairly closely around the trunk of the axostyle.

In the spiraled part the chromophile element at the inner edge is a band nearly the full width of the parabasal, so that the inner edge is flat (pl. 4, fig. 35). This narrows at the anterior end of the spiral, passes along the nuclear edge of the longitudinal part for a short distance, and then, while still far from the anterior end, separates from the other substance and passes independently by the most direct route to the blepharoplast (pl. 4, fig. 34; fig. B, 13). The anterior part of the parabasal, consequently, does not include a chromophile element.

The chromatic shield is typical, a group of closely set small granules cresta-shaped in optical section reaching to the blepharoplast.

The part of the capitulum between the anterior end of the nucleus and the anterior edge of the body was incrusted in all material examined from one colony of termites (T-4545) with deep-staining granules, some spherical, some elongated. These granules marked out the limits of the capitulum very clearly. Granules of the same size and form were abundant throughout the cytoplasm, sometimes gathered into irregular-shaped masses. These granules were absent from the capitulum of specimens from T-4543, in which the chromatic shield was seen most clearly. The granules of the chromatic shield are much smaller and more regularly rounded than the capitular granules.

The trunk of the axostyle (pl. 5, figs. 36, 37) is not of the usual *Devescovina* type. It is not very stout in any part, but does not taper to a filament within the cytoplasm as in most species of *Devescovina.* It extends through the cytoplasm straight or smoothly curved; there is no sinuosity in its course. At the posterior end of the cytoplasm there is no cusplike enlargement, which is a very prominent feature of a large species of *Foaina* in this termite, but the diameter of the trunk at that point is but little less than at its anterior end. There is then a part which projects from the body. The projection is characteristic of *D. vestita.* The length of the projection varies from very little up to about 10μ.

There is no differentiation in the distribution of cytoplasmic inclusions as in *D. tendicula.* One specimen (pl. 5, fig. 38) contained four small oxymonads, all normal in appearance, but no others were seen with any ingested material other than wood.

The adherent spirochaetes on the surface of the entire region posterior to the nucleus and parabasal body (pl. 5, fig. 36) are unusually thickly distributed for *Devescovina,* the situation more closely resembling that in certain species of *Caduceia.*

The *Fusiformis*-like microörganisms that adhere longitudinally to the surface (pl. 5, fig. 37) are different in morphology and arrangement from those on most species of *Devescovina.* The most anterior part of the body, where spirochaetes are absent, is also free from the rods. At the boundary of this area the rods are often lined up in an orderly manner: all longitudinal, more or less evenly spaced in relation to one another, with the anterior ends aligned. Posterior to this their arrangement, although often longitudinal, is more irregular in both direction and spacing. It would be impossible to mistake the rods for regular longitudinal striations of the surface, an error which would be possible in most other species of *Devescovina.* Most of the rods range from 2.5 to 9μ in length, lengths of 4 to 6μ being frequent. The rods on most species of *Devescovina* are longer and more slender.

## **Devescovina exilis** sp. nov.

(Pl. 5, fig. 39; fig. B, 15)

***Devescovina striata*** **Foà var.** ***hawaiensis*** **Janicki, small form,** ***partim,*** **Janicki, 1915, Zeitschr. w. Zool., 112: 575, text fig. 2 (?).**

***Type host.—Neotermes connexus*** **Snyder. Hawaii.**

**T-306. (Fullaway.) (Syntype slides TP-208:4, 8.)**

***Diagnosis.*****—Length 40 (32–56)μ; width 7 (6–10)μ; trailing flagellum narrow band-shaped, maximum breadth 0.5–1μ; cresta length 3.5 (2.3–4.1)μ, anteromedial edge 1.5–2μ; parabasal body turned usually once or less, rarely a little more, posterior part often extended**

**out straight in cytoplasm; trunk of axostyle surrounded in posterior part by one or two small, siderophile rings; nucleus 4.9 (4.2–5.3) by 3.2 (2.3–4)$\mu$; adherent rods of long, slender, longitudinal type; small tuft of long spirochaetes often present on anterior end.**

Janicki (1915) distinguished two forms of *D. striata* var. *hawaiensis,* one slenderer and more abundant, the other broader and infrequent. The slenderer form included both the species distinguished here as *D. exilis,* and most individuals of *D. hawaiensis.* His text figure 2 resembles the former species more than the latter.

The length of *D. exilis* is about equal to that of *D. hawaiensis,* but the breadth is much less, the ratio being about 1:6 as compared to 1:3.

There is a constant difference in the crestas, apparently without intergradation. They are similar in shape of the anterior parts, but that of *D. exilis* (fig. B, 15) is shorter and more sharply tapered to a point.

The parabasal body resembles that of the smaller individuals of *D. hawaiensis.* None has been observed with a larger number of turns than one or very little more. It often curves around the axostyle, partly completing one loop, but instead of coiling further extends straight out for a short distance; or it may complete one loop or slightly more. The posterior part does not taper as in *D. cometoides.* A type of parabasal form frequent in this species is shown in Janicki's text figure 2.

The suspensorial lamella, which is a conspicuous feature in suitably stained specimens of *D. hawaiensis,* seems to be represented only by an inconspicuous filament or to be absent altogether in *D. exilis.*

The two species of *Devescovina* in *Neotermes connexus* can usually be distinguished from one another by nuclear structure alone. In *D. exilis* the central chromatin mass is usually somewhat rectangular in form, and one side of the mass is extended posteriorly to a point (pl. 5, fig. 39). The pointed projection reaches the nuclear membrane, which possibly is pushed out, and constitutes a triangle along the anterior end of the trunk of the axostyle. In *D. hawaiensis* there is a deeper-staining triangular structure on the trunk of the axostyle, in a corresponding position, which is separated by a space from the central chromatin mass (pl. 9, fig. 63). In the preparations examined, a clear space separates the nuclear membrane from the central chromatin mass, but usually this space is not so broad and conspicuous as that in *D. hawaiensis.*

On the anterior end of *D. exilis* there is often a small tuft of spirochaetes similar to that on *D. cometoides,* but there are no spirochaetes on other parts of the body. *D. hawaiensis* has no regularly adherent spirochaetes.

It would be easy to suggest that *Devescovina exilis* is merely an undeveloped form of *Devescovina hawaiensis* in which the cresta, suspensorial lamella, and parabasal body are less advanced in development. In the light of the demonstration to be given later in this series of papers that the organelles reach almost or quite full development before cytoplasmic division, the probability of this is decreased, but the interpretation remains plausible. However, I have distinguished the two species after a careful consideration of the constant association of all the differential characters and after an effort to bring my decision into harmony with the results of studies of many devescovinids.

### **Devescovina lepida** sp. nov.

(Pl. 6, figs. 44–47; pl. 7, fig. 48; fig. C, 1)

*Type host.*—*Calcaritermes brevicollis* (Banks). Panama.
T-206. Barro Colorado. (Syntype slides TP-120:9; 118:1.)
T-125, 130, 197. Same locality.

*Additional hosts*—
*Calcaritermes emarginicollis* Snyder. Costa Rica.
T-171. Estrella. (Homosyntype slide TP-106:24.)
*Calcaritermes nearcticus* Snyder. Florida.
T-531. Bartow. (E. M. Miller.) (Homosyntype slide TP-534:2.)
*Calcaritermes parvinotus* Light. Mexico.
T-265. Colima. (Light 183 Me.) (Homosyntype slide TP-225:8.)
*Cryptotermes longicollis* (Banks). Panama. (Generic det. by Emerson.)
T-223. Taboga Island. (Homosyntype slides TP-137:40, 26, 7.)
T-225. Same locality.
*Neotermes castaneus* Burmeister. Florida.
T-530. Pine Crest. (Homosyntype slide TP-533:30.)
*Neotermes holmgreni* Banks. Panama.
T-101. Barro Colorado. (Homosyntype slide TP-31:21.)
T-222. Taboga Island. (Homosyntype slide TP-134:8.)

*Diagnosis.*—(From type host): length 50 (36–39)μ; width 19 (14–26)μ; trailing flagellum a broad ribbon, about 1.4–2μ; cresta length 2.8 (2.5–3.5)μ, anteromedial edge almost the same, posteromedial edge about 1μ; parabasal body with 1–3 turns, usually 1½–2; nucleus 5.2 (5–5.7) by 3.9 (3.6–4.2)μ; adherent rods of long, slender, parallel type; no adherent spirochaetes. (From *Cryptotermes longicollis*): length 52 (36–65)μ; width 14 (9–26)μ; cresta 3.1 (2.9–3.5)μ; parabasal turns 1½ (1¼–2½); nucleus 5.5 (5.2–6) by 3.9 (3.1–4.2)μ.

*Devescovina lepida* is relatively large and has a trailing flagellum (pl. 6, fig. 45; pl. 7, fig. 48) almost as broad as that in any other species; but the cresta is a comparatively small structure. The shape of the cresta is unusual (fig. C, 1). The anteromedial edge, instead of being the shortest of the three edges, as in most species of *Devescovina,* is almost as long as the external edge. The posteromedial edge is very short, so that the structure has the form of a rather narrow triangle with the apex at the blepharoplast, two equal sides, and a shorter base.

The spiral of the parabasal body is open to the degree that there is some space between it and the trunk of the axostyle (pl. 6, fig. 47), and in this numerous granules were present in specimens from *C. brevicollis* and *C. emarginicollis* (pl. 6, fig. 46). The granules were constant in occurrence and stained readily with both Delafield's and Heidenhain's haematoxylin.

The parabasal body at the first turn is usually somewhat stouter than in the more posterior parts (pl. 6, fig. 47), but there is not so distinct a taper as in *D. cometoides.* The longitudinal part is slenderer, and there is some variation in its size and in the enlargement at the anterior end. This enlargement was more prominent in specimens from *C. brevicollis* and *C. emarginicollis* than in those from *C. longicollis* and *N. holmgreni,* but in devescovinids in general it is a somewhat variable characteristic. The chromophile element is often apparent in the first part of the spiral, as broad as the full width of the inner edge.

The trunk of the axostyle tapers to a slender filament which stains intensely with iron-haematoxylin in heavily stained material. In some specimens a slender spiral filament, believed to be the persisting paradesmose, has been observed around the trunk of the axostyle (pl. 6, fig. 45).

The central chromatin mass of the nucleus is prolonged posteriorly in a pointed protuberance toward the trunk of the axostyle (pl. 6, fig. 46), and there is no separate conical element.

### **Devescovina arta** sp. nov.

(Pl. 5, fig. 40; pl. 6, figs. 41–43; fig. B, 16)

*Type host.—Glyptotermes angustus* Snyder. (= *G. barbouri* Snyder.) Panama.
T-216. Barro Colorado. (Syntype slides TP-123:2; 124:6.)

*Additional hosts—*

*Glyptotermes minutus* Kemner. Ceylon.
T-313. (Cleveland. Collier.) (Homosyntype slide TP-264:2, 3.)

*Neotermes castaneus* Burmeister. Florida.
T-530. Pine Crest. (Homosyntype slide TP-533:29.)

*Diagnosis.*—(From type host): length 42 (32–53)μ; width 8 (6–12)μ; trailing flagellum a broad ribbon, 1.5 (1–2)μ; cresta formed as in *D. lepida*, length 2.8 (2–3.3)μ; parabasal body turned closely around trunk of axostyle 1–2 times, usually 1½ or less, tapered posteriorly to a blunt point; nucleus 4.4 (4–4.9) by 3 (2.7–3.6)μ; adherent rods of long, slender, parallel type; no adherent spirochaetes. (From *Glyptotermes minutus*): length, most specimens, 37 (26–47)μ; width 9.5 (6–14)μ, unusually large specimens 50–73 by 10–20μ; length of trailing flagellum 60–75μ, width about 1.5μ; nucleus 5 (4.8–5.7) by 2.5 (2.1–3.1)μ.

*Devescovina arta* is much like *D. lepida,* agreeing exactly with it in cresta and trailing flagellum. The size is less in length and particularly in width; different enough, probably, to be significant. There are, however, some specimens in *Glyptotermes minutus* which are as large as the larger specimens of *D. lepida.* In general, the body is narrower in relation to its length.

The only cytological difference observed is in the parabasal body. The anterior part of the parabasal body (pl. 6, fig. 42; fig. B, 16) is hardly more than a stout filament, which stains deeply with iron-haematoxylin after Flemming's fluid, and also with Delafield's haematoxylin after Schaudinn's fluid. Delafield's haematoxylin would be expected to show this part of the parabasal completely, as it did the stout corresponding structure in a species of *Metadevescovina* on the same slides. Furthermore, it passes directly to meet the blepharoplast, without extending around on the anterior face of the nuclear membrane or undergoing any enlargement as in many species of *Devescovina.*

At the beginning of the spiral, the parabasal is sharply enlarged (pl. 6, fig. 42). The inner edge is flat and for its full breadth stains deeply with iron-haematoxylin. In its posterior portion the parabasal tapers and is bluntly pointed as in *Devescovina cometoides.* In *D. arta* from *Glyptotermes angustus* it turns from 1 to 2 times, but more than 1½ turns are exceptional. In smaller individuals it is commonly a little more than 1 and in larger individuals 1½. In specimens from *Glyptotermes minutus,* the spiral more frequently reached 1½ or 2 turns, and sometimes exceeded this by about half a turn. The coiling is very close, much more so than in *Devescovina lepida.*

The spiral is drawn out, leaving more space between adjacent coils, in some specimens. This was especially frequent in the material from *Glyptotermes minutus* (pl. 5, fig. 40; pl. 6, fig. 43), which was so stained that only the chromophile element was demonstrated. Only two slides from that host were available, and study of additional material is especially desirable. The technique not being the same, it is not certain that the incompletely demonstrated parabasal of the flagellate from *G. minutus* really is the same in morphology as the one in the flagellate from *G. angustus.* There does seem to be the difference in degree to which the spiral is drawn out.

In its stoutest part the parabasal often gives an illusion of being double; in Flemming–iron-haematoxylin material especially, the black-stained substance may be localized on the inner edge and sides, leaving a lighter part in the middle of the outer edge. The last substance to destain is the bandlike chromophile element at the inner edge.

No granules like those present within the parabasal spiral of *D. lepida* from *Calcaritermes brevicollis* and *C. emarginicollis* are present in *D. arta.*

The axostyle tapers to a slender filament, is often curved or sinuous in its course through the cytoplasm (pl. 6, fig. 41), and sometimes lies close to one side of the body posteriorly. In a few specimens its end was recurved although the body was pointed posteriorly as usual.

The chromatin mass of the nucleus is extended to a point posteriorly. The anterior end of the nucleus is often very close to the blepharoplast and sometimes is drawn out in a point toward it. There the membrane may apparently be applied to the blepharoplast, and the chromatin mass may extend to it. There is sometimes recognizable a filament extending from the blepharoplast to the nuclear membrane, when this is at any distance from the blepharoplast.

An unusual situation, in which the trailing flagellum is completely enclosed in the cytoplasm, is shown in plate 6, figure 43. This phenomenon has been noted in occasional specimens of a number of devescovinids.

### **Devescovina vittata** sp. nov.

(Fig. C, 2, 3; fig. D, 4)

*Type host.—Kalotermes* (s. str.) sp. nov. Tanganyika Territory.

T-3025. West of Ngorongoro Crater, at edge of Serengetti Plains. (Syntype slides TP-2044:15, 17, 5.)

*Diagnosis.*—Length 62 (48–80)μ, exceptionally 110μ; width 30 (22–38)μ; trailing flagellum a band often reaching a maximum breadth of about 1μ; cresta length 6.5 (6–8)μ, anteromedial edge 3 (2.5–4)μ, more or less straight-sided with no abrupt taper; parabasal body with a moderate-sized hook anteriorly, spiraled closely around trunk of axostyle 2–5 times, 2–3½ in most specimens, average 3; granules of chromatic shield present, but not so definitely organized as in some species; axostyle of typical form; nucleus 6–8 by 3.5–5.5μ, averaging 7 by 4.5μ; surface, except for the most anterior part, bearing long, slender microorganisms; no spirochaetes regularly adherent to surface.

*Devescovina vittata* is noteworthy because of its relatively large size. The ratio of width to length is about 1:2, which is unusual in the genus. On most smears the posterior end is rounded, but in well-preserved material it is extended to a point. The papilla is relatively small.

The trailing flagellum is a band of moderate breadth. That of *D. lemniscata* is typically a broader band. *D. lemniscata* from *Neotermes insularis* is of similar large size, but average specimens of *D. vittata* are considerably larger than most specimens of *D. lemniscata.* In a number of specimens on the smears the trailing flagellum was completely enclosed in the cytoplasm.

The cresta (fig. C, 2, 3) is broader in its posterior part than in many species of *Devescovina.* It is bluntly instead of sharply pointed, and in many specimens it is truncate posteriorly as if a piece had been broken off. The differences in shape of the cresta between *D. vittata* and the largest specimens of *Devescovina hawaiensis* in *Neotermes connexus* are constant and marked. They are sufficient to separate the two taxonomically, although in other features these species are much alike.

The parabasal body is turned sharply in a well-developed hook on the anterior surface of the nuclear membrane. The chromophile element is sharply differentiated and heavy staining. It is a fairly broad band along the inner edge of the anterior part of the spiral, but becomes more slender toward the posterior end. In the posterior part of the longitudinal portion it tapers rapidly to a filament, then separates from the other substance and passes independently to the blepharoplast, along the anteromedial edge of the cresta. The first turn is sometimes broader than the others and partly covers the next turn.

The chromatic shield was not so clearly recognizable as in *Devescovina fissa, D. tendicula,* and other species. A similar grouping of granules was observed in many specimens along the nuclear membrane, beginning close to the anteromedial edge of the cresta (fig. C, 2). This is a band one granule thick reaching to near the posterior end of the nucleus. The granules were not seen in many specimens, which may not have been favorably stained for the structure.

Posterior to the nucleus there is a prominent, deep-staining subtriangular projection into or along the trunk of the axostyle, separate from the chromatin mass.

In *D. vittata,* as in *D. tendicula,* there is a dense grouping of small wood particles in an otherwise clear region alongside of and posterior to the parabasal body (fig. D, 4) but in *D. vittata* this region is relatively much more limited both laterally and longitudinally, although the difference between it and the rest of the cytoplasm is just as marked as in *D. tendicula.*

### **Devescovina striata** Foà

(Pl. 7, figs. 49–51; fig. C, 6)

*Devescovina striata* Foà, 1905, Atti. R. Accad. Lincei (5), 14:545.—Janicki, 1915, Zeitschr. w. Zool., 112:632, text fig. 11.—Kirby, 1926, Univ. Calif. Publ. Zoöl., 29:104, fig. A, 1.

*Devescovina paralemniscata* Calkins, 1936, Puerto Rico Jour. Pub. Health and Trop. Med., 12:170, text fig. 1.

*Type host.*—*Cryptotermes grassii* Silvestri, *nomen nudum.* Chile.

T-320. Iquique. (Silvestri.) (Xenosyntype slide TP-325:1.)

*Additional hosts*—

*Cryptotermes brevis* (Walker). Mexico. Puerto Rico. Peru.

T-261. (Light 75.) Colima, Mexico. (Homosyntype slides TP-219:31, 33, 34, 20.)

T-240. Puerto Rico. (Homosyntype slide TP-155:3.)

T-4600. Lima, Peru. (Homosyntype slide TP-3283:5.)

*Cryptotermes piceatus* Snyder. Hawaii.
T-321. (Fullaway.) (Homosyntype slide TP-207:3.)
*Cryptotermes darwini.* Light. Galápagos Islands.
T-335. (Light 1311 Ga.) James Is. (Homosyntype slide TP-275:5.)
T-238. (Beebe.) Gardner Is. (Homosyntype slide TP-153:14.)
*Cryptotermes* sp. South Africa.
T-4011. Durban. (Homosyntype slides TP-2072:8, 13; 2070:2, 17.)

*Diagnosis.*—(From type host, original): length 27 (20–37)μ (according to Foà, mean length 40μ); width 13 (11–18)μ; trailing flagellum band-shaped, often 1–1.5μ wide; cresta triangular, straight sided, length 5.2 (4.5–6)μ, anteromedial edge about 2.5μ; parabasal body not seen well in material (see below for spiral); nucleus 4.2 by 2.5μ; adherent rods of long, slender, parallel type; no adherent spirochaetes. (From *Cryptotermes brevis*): length 47 (31–61)μ; width 15 (11–18)μ; trailing flagellum 1–1.5μ maximum breadth; cresta length 5.3 (5–6.5)μ; parabasal turns 1¾ (1–2½); nucleus 4.7 (3.2–6) by 3.5 (2.6–5)μ; no adherent spirochaetes. (From *Cryptotermes piceatus*): length 45 (37–57)μ; width 15 (10–20)μ; cresta 5.7 (5–6.5)μ, anteromedial edge 3 (2.5–3.5)μ.

Emerson has informed me, in a personal communication, that the name *Cryptotermes grassii* Silvestri is not in the literature on termites. It appears, however, in the papers of Janicki (1911, 1915), who reported, as Foà had done, that the termites were sent by Professor De Vescovi in 1905. Evidently Silvestri had seen and assigned a name to the insects, but his account has not been published, as he himself communicated to me. The faunule of the termite is the same as that of *Cryptotermes brevis* (Walker) and *C. piceatus* Snyder.

Sutherland (1933) listed *Devescovina striata* Foà from *Neotermes insularis* and *Kalotermes oldfieldi* var. *chryseus,* both of Australia; but in the text she stated that the *Devescovina* in *Neotermes insularis* is probably identical with *Devescovina striata* var. *hawaiensis* from *Neotermes connexus.* Sutherland apparently gave little consideration to the taxonomic characteristics of *Devescovina* as recognized by me, and did not even mention the cresta. It would have been impossible to identify with certainty any devescovinid with *Devescovina striata* or the so-called variety *hawaiensis* without examining specimens of those species. Therefore no further consideration can be given to Sutherland's records of the occurrence of *Devescovina striata.* The species of *Devescovina* in *Neotermes insularis* is *D. lemniscata.*

*Devescovina paralemniscata* Calkins was recorded by him from a termite at San Juan, Puerto Rico, which was identified by Dr. T. E. Snyder as *Cryptotermes brevis. D. striata* has been identified by me as the only species of the genus in certain termites of the species *C. brevis* from Mexico and Puerto Rico, after comparison with specimens on a smear from the type host, *Cryptotermes grassii.* Furthermore, Calkins' description of the trailing flagellum and cresta fits *D. striata.*

Calkins stated that "striations" are absent from *D. paralemniscata;* that the parabasal body is only a filament and does not encircle the axostyle; and that the axostyle is only about three-fourths the length of the body. The so-called striations are likely to be overlooked in preparations unfavorable for their demonstration, which probably accounts for Calkins' failure to see them; they are present in all species of *Devescovina* studied by me in preparation of this monograph. The parabasal body would probably have been seen if Delafield's haematoxylin had been used. The filamentous posterior part of the axostyle possibly was not visible, though most likely it was present, in Calkins' preparations. The presence of a papilla is a generic characteristic, and it is unlikely that it was absent, as Calkins reported. My diagram of *D. lemniscata* (Kirby, 1926, fig. C) was incorrect and misleading in not showing a papilla. The anterior flagella in *D. striata* are much longer than those Calkins represented in *D. paralemniscata;* according to my observations, all species of the genus have uniformly long anterior flagella.

Calkins (1936) listed *Devescovina striata* Foà from another termite of San Juan, Puerto Rico, obtained from a pine box. According to Calkins, the flagellates were of the same types as those found in *Cryptotermes brevis;* but he gave different species names to the flagellates of the two termites. It is probable that both the hosts were *Cryptotermes brevis;* certainly it is unlikely that the polymastigotes would occur in *Heterotermes,* which he suggested the termite may have been. I have observed no Devescovininae or Calonymphidae in any Rhinotermitidae, although I examined 29 species in 7 genera (Kirby, 1937*a*).

The characteristics given by Foà for *D. striata,* except for the rather slender trailing flagellum, might apply to almost any species of *Devescovina.* With respect to the flagellum, however, she was inaccurate; it is a rather broad band. She neither figured nor mentioned the cresta. The striations, which led to the specific name, probably occur on all species of *Devescovina.* The specimens on Silvestri's smear from *C. grassii* were smaller than those measured by Foà, but probably they were undersized. The size of specimens in *C. brevis* and *C. piceatus* agreed more closely with the measurements given by Foà and Janicki.

The blepharoplast is a moderate-sized mass uneven in outline and clearly composed of several granules (pl. 7, fig. 50). Calkins stated that there are 1 to 3 granules.

The cresta of *D. striata* in the type host and in other hosts is occasionally straight sided, or nearly so. Usually, however, the external edge is more or less convex and the posteromedial edge more or less concave (pl. 7, fig. 50; fig. C, 6). There is no sharp bend inward at the anterior part of the posteromedial edge, as in *D. hawaiensis* (fig. C, 9) and certain other species. In some specimens the posteromedial edge is little if any longer than the anteromedial edge. Often it is 1½ to 2 times this length.

No chromatic shield was observed in material which might have been expected to show it if it were present.

Janicki (1915) stated that the parabasal body in *Devescovina striata* almost without exception turns twice around the axostyle. In the flagellates from *Cryptotermes brevis* the number of turns ranges from 1 to 2½, usually amounting to about 1½ to 2. It is rounded posteriorly, where it diminishes little, if any, in diameter. The anterior part, which passes longitudinally along the nucleus near the cresta, is somewhat slenderer than the first part of the coiled portion. At the anterior end of the nucleus, at a short distance from the blepharoplast, there is the rounded or somewhat enlarged anterior end of the parabasal body. In many specimens it is turned in a short hook anteriorly. The chromophile filament passes to the blepharoplast, leaving the longitudinal part some distance from the anterior end (fig. C, 6). Calkins observed this chromophile element and believed that it represented the entire parabasal body, but obviously he overlooked most of the structure.

The *Fusiformis*-like microörganisms for which the species received its name are of the long, slender type found on most species of *Devescovina.* There are no adherent spirochaetes.

### **Devescovina lemniscata** Kirby

(Pl. 7, fig. 52; pl. 8, figs. 56–61; fig. C, 5; fig. E, 1)

*Devescovina lemniscata* Kirby, 1926, Univ. Calif. Publ. Zoöl., 29:103, figs. B, C, plate 1, figs. 1–11.

*Devescovina damanensis* de Mello and de Brito, 1929, Arqu. Esc. Med.—Cirurg. Nova Goa, (A) fasc. 5:699, figures.

*Type host.*—*Cryptotermes hermsi* Kirby. Fanning Island.
T-9. (Syntype slides TP-1:3, 2; 5:1, 3; 6:1, 2.)

*Additional hosts*—
*Cryptotermes breviarticulatus* Snyder. Panama.
T-230. Taboga Island. (Homosyntype slides TP-141:1, 22.)
*Cryptotermes domesticus* (Haviland). Singapore.
T-4589. (Homosyntype slide TP-3272:3.)
*Cryptotermes dudleyi* Banks. Panama.
T-239. Barro Colorado. (Homosyntype slides TP-163:1, 5, 9; 168:1.)
*Cryptotermes fatulus* Light. Galápagos Islands.
T-330. (Light 1303 Ga.) Vilamill, Albemarle Is. (Homosyntype slide TP-295:5.)
T-334. (Light 1302 Ga.) James Is. (Homosyntype slide TP-269:3.)
*Cryptotermes queenslandis* Hill. Australia.
T-519. (Hill 3492.) S. W. Australia. (Homosyntype slide TP-519:14.)
*Cryptotermes* sp. Tanganyika Territory.
T-1013. Tanga. (Homosyntype slide TP-1023:36.)
*Cryptotermes* sp. Kenya Colony.
T-1075. Taveta Forest. (Homosyntype slide TP-1063:7.)
T-1091. Taveta Forest. (Homosyntype slide TP-1079:1.)
*Cryptotermes* sp. nov. Mauritius, Madagascar.
T-4525. Reduit. (Homosyntype slide TP-3204:16.)
T-4506. Tamatave. (Homosyntype slide TP-3190:6.)
*Cryptotermes* sp. nov. Java.
T-4553. Tapos. (Homosyntype slide TP-3237:2.)
*Cryptotermes* sp. Ecuador.
T-4609. (Von Hagen 19.) Hac de Tenguel. (Homosyntype slide TP-3282:2.)
*Kalotermes* (s.l.) sp. Portuguese India.
T-317. (De Mello.) Damaum. (Homosyntype slide TP-323:5.)
*Glyptotermes tuberculatus* Froggatt. Australia.
T-4608. (Hill. Cleveland.) (Homosyntype slide TP-3284:19.)
T-507 (Hill 3187.) (Homosyntype slide TP-507:1.)
*Glyptotermes* sp. Java. (Probably *caudomunitis,* acc. to Emerson.)
T-4560. Bandjar. (Homosyntype slide TP-3212:4.)
*Neotermes castaneiceps* Sjöstedt. Madagascar.
T-4505. Tamatave. (Homosyntype slides TP-3191:7, 11.)
T-4476. Near Ihosy. (Homosyntype slide TP-3173:6.)
*Neotermes* sp. nov. Madagascar. (Near, or possibly same as, *castaneiceps.* Emerson.)
T-4468. Near Ambovombe. (Homosyntype slide TP-3171:2.)
*Neotermes insularis* (White). Australia.

T-522. (Hill 3231.) Ravenshoe, Queensland.

T-308. (Hill.) (Homosyntype slides TP-320:24, 95, 197.)

*Neotermes larseni* Light. Cocos Island.

T-322. (Light 1289 Co.) Wafer Bay. (Homosyntype slides TP-278:2, 3.)

*Neotermes longus* (Holmgren). Madagascar.

T-4395. Near Besangoa. (Homosyntype slides TP-3141:12, 6.)

*Diagnosis.*—(From type host, revised): length 35 (21–51)μ; width 12.5 (9–17)μ; trailing flagellum a broad band; cresta length 8 (7–9)μ, anteromedial edge about 2.5μ; parabasal turns about 1 (¾–2); nucleus 6 (5.5–7) by 3.5 (3–4)μ; no adherent spirochaetes. (From *Cryptotermes dudleyi*): length 42 (28–63)μ; width 16 (10–24)μ; cresta 8.7 (7–10)μ; nucleus 5.2 (5–5.7) by 4.1 (3.6–4.7)μ. (From *Cryptotermes breviarticulatus*); length 46 (36–61)μ; width 17 (9–25)μ. (From *Neotermes insularis*): length 42 (22–68, exceptionally 78)μ; width 16 (9–31, exceptionally 37)μ; cresta 9 (7–13)μ, anteromedial edge 2.5–3μ; parabasal turns 1½–3, occasionally 4; nucleus 6 (4.9–7.3) by 5 (3.9–5.7)μ. (From *Kalotermes* sp. T-317. *D. damanensis*): length 47 (32–67)μ; width 20 (12–27)μ. (From *Cryptotermes* T-1091): some spirochaetes adherent to all parts of body except the anterior end.

In my original description of *Devescovina lemniscata* (1926) there are errors that violate certain fundamental principles of devescovinid morphology; these are corrected in the following account. The length of material from the type host is somewhat greater than that previously reported, but still the specimens are smaller on the average than those in the other hosts. In the original description the two forms—one broad, with included axostyle; the other small, with projecting axostyle—were incorrectly distinguished. The "broad form" more closely represents the normal form of the flagellate, except that the posterior end is usually more pointed. The smaller form was abnormal, owing to plasmotomy; the axostyle does not normally project free of the cytoplasm.

In *Neotermes insularis* there are present, along with smaller specimens and connected with them by a transitional series, a greater number of larger forms than have been encountered elsewhere. These reach a length of 79μ and a width of 37μ, have three or four parabasal coils, but differ in no cytological characteristic from the more average-sized *D. lemniscata.*

In this species there is always a prominent papilla (pl. 8, fig. 58) along the anterior edge of which the roots of the anterior flagella adhere. The original description was incorrect in regarding the papilla as an inconstant feature and in showing the anterior flagella in some figures as becoming free directly. Only when the papilla is extended can it be seen in its entirety, and in the material examined this usually was not the case.

The blepharoplast group is composed of several granules. These appear large and closely aggregated in heavily stained material, small and more distinctly separated in more lightly stained material. The original description, which was influenced by Janicki's account, was incorrect in considering the blepharoplast to be a group of minute granules enclosed within a membrane. There apparently is a matrix which stains with iron-haematoxylin more lightly than the granules, so that these seem to vary in size with depth of staining.

The trailing flagellum is usually a broad ribbon in its middle part (pl. 7, fig. 52; pl. 8, fig. 60). Measurements of fixed specimens from *Cryptotermes* *dudleyi* gave a range in maximum width from 1.5 to 2–3μ, averaging about 1.7μ. In some living specimens from *Neotermes insularis,* the trailing flagellum had a breadth of 3μ. In *Cryptotermes* sp. from Taveta Forest, T-1075, all slides had *D. lemniscata* with the broad band-shaped trailer; but the series from T-1091 had some slides bearing specimens with a cordlike trailer, only one type on a slide. There is a possibility that those with a cordlike trailer represent a variant of *lemniscata,* though typical *lemniscata* were not present on the same slides. In this paper, however, they have been classed as *D. glabra.* There seemed to be some differences between the two forms in adherent spirochaetes, which occurred mainly on the anterior end only in the one called *D. glabra* and on more posterior parts of the body in *D. lemniscata.*

The cresta (fig. C, 5) is one of the longest in the species of *Devescovina* which I have studied. Its proximal edge is broad, straight, and is connected by a short filament at its outer angle to the blepharoplast. Posteriorly, after a sharp initial decrease in width, it tapers gradually to the bluntly pointed distal end. The posterior part of the cresta sometimes, but not often, protrudes outside the usual contour of the body (pl. 8, fig. 56); when it does so, some of the cytoplasm of the body is carried with it. The boundary of the body is normally external to the cresta.

The larger cresta is the only notable difference between *D. lemniscata* and *D. striata.* That difference is usually marked, but there is sometimes difficulty in separating the two species. This is particularly true in *Cryptotermes fatulus,* in which the species of *Devescovina* has a cresta of intermediate type. It resembles the smaller crestas of *lemniscata* more, however, than the average of *striata.*

Detailed observations have been made on the axostyle in stained material from *Cryptotermes dudleyi.* The trunk decreases in diameter posteriorly until it is reduced to a filament in the posterior part of the body. The edges of the trunk appear as well-defined lines, but the substance of the trunk usually does not stain. The body is almost always drawn out into a point posteriorly, and the axostyle extends into this pointed portion. The end of the axostyle does not normally project free from the cytoplasm.

Usually the axostyle does not extend from the nucleus to the posterior end of the body as a straight rod. Often it is longer than the corresponding length of the cytosome, so that it is bent or sinuous, especially in its posterior portion. Occasionally it is bowed outward so as to approach one side of the body; in a few specimens it is close to one edge for most of its extent.

When the posterior end of the body is broadly rounded, the axostyle is curved back in the cytosome. The fact that the length of the axostyle is greater than that of the body in such specimens shows that the elongated shape is the typical one. It is clear, however, from the position of the axostyle that the rounding out could not be the result of an accident in smearing, or of a sloughing off of cytoplasm. Occasionally there is a slender, taillike process containing the axostyle; this is the result of a sloughing off of cytoplasm.

The trunk of the axostyle enlarges somewhat anteriorly and ends abruptly against the posterior end of the nucleus. As the enlargement appears the same no matter what side of the body is turned uppermost, it must be circular in cross section. Extending into the middle of the trunk is a deep-staining conical structure.

The axostyle is continued on one side of the nucleus as a flattened, spoon-shaped capitulum. This lies close against the nuclear membrane, and it is possible to distinguish only its edges. At its anterior end the capitulum narrows and approaches the blepharoplast, but it appears to pass to one side of this rather than actually to meet it. The edge of its extension into the papilla is parallel to the roots of the anterior flagella, appearing as a lamella that turns posteriorly at the tip and approaches the nuclear membrane.

In flagellates in different hosts there is variability in the number of turns of the parabasal body. In *Cryptotermes hermsi* there usually is only about 1 turn (pl. 8, fig. 61), sometimes as much as 2. *In Neotermes longus* many flagellates have 1½ turns; none were seen with more than 2. The larger specimens in *Neotermes insularis* have 2½ to 4 turns. The posterior end of the parabasal is not tapered to a blunt point as is usual in *D. cometoides,* which in some hosts is associated with *D. lemniscata.*

The chromophile element, which appears as a band in some material, is present at the inner edge of the spiral (fig. C, 5). About the middle of the longitudinal part, or more posteriorly, it separates and passes directly to the blepharoplast. The remaining substance continues against the nuclear membrane. At the anterior end there is often an enlargement (pl. 8, fig. 59). Frequently, especially in larger individuals, the end is bent in a hook across the anterior end of the nucleus.

In the original description the anterior part of the parabasal was not described correctly. The technique used was effective in demonstrating only the chromophile element of the anterior part. This was traced correctly along the anteromedial edge of the cresta to the blepharoplast, but the other substance was not seen. I was, consequently, misled into stating that the parabasal body is gradually narrowed to its anterior attachment; whereas actually the anterior part, though somewhat flattened, is as broad as the coiled part.

Very often a space of variable width is present in the nucleus between the chromatin mass and the membrane. However, in some specimens on certain slides there is no space; in these nuclei there is no structural discontinuity between the chromatin mass and the deep-staining, conical structure that seems to be fitted into the end of the trunk of the axostyle. The posterior conical structure stains even more intensely than the nucleolus with iron-haematoxylin, and is black when the chromatin is gray.

An aggregate of granules or short rods, like that characteristic of *Devescovina glabra,* is present just posterior to the parabasal body in *D. lemniscata* from *Neotermes longus* and *Neotermes castaneiceps* (fig. E, 1). The very broad trailing flagellum clearly distinguishes this form from *D. glabra.*

The *Fusiformis*-like microörganisms are of the usual long, slender type (pl. 7, fig. 52; pl. 8, fig. 60). No adherent spirochaetes are present in most hosts; an exception is noted in the diagnosis.

Observations were made on living flagellates from *Neotermes insularis* and to some degree from *Cryptotermes dudleyi.* Those reported below were obtained, unless it is otherwise stated, from the former host.

The three slender anterior flagella extend from the pointed end of the papilla at various angles to the body, from straight forward to diagonally in the posterior direction; the "resting" position is diagonal anteriorly at an angle of about 45 degrees. In their proximal portions the flagella are commonly united, almost or quite to the end, into a whip. As the material becomes moribund, the free parts of the flagella separate completely.

The anterior flagella are moved very actively. The movements consist mostly in lashings of the whip as a whole and not in vibrations or undulations of the individual flagella. The lashings of the whip are caused by lateral bending movements of the papilla. The flagella are extended somewhat as a rope might be thrown out to its full extent by an impulse originating in a quick movement of the arm. They are capable, however, of bending movements. When, in slowly moving moribund animals, the whip is advanced, the flagella may be observed to curl slowly posteriorly toward the body before the next lash of the whip takes place. This curling may take place independently in each of the three flagella.

The vigorous lashing of the papilla and anterior whip impart a jerky movement to the flagellate. At times, however, the papilla and whip may be motionless. The papilla is then turned back so that the point is not visible, and the adherent bases of the flagella pass across the anterior portion of the body. Beyond the point where they become free, the flagella are often curved back and extend transversely across again in front of the body. This position is commonly taken when the flagellates die; but it may also be taken when the flagellates are active but the whip is motionless. In such animals forward progression may take place, the impulse coming entirely from the undulating movements of the trailing flagellum. This behavior has also been observed in *Devescovina lemniscata* from *Cryptotermes dudleyi.* At other times the trailing flagellum may be quiet or even absent, the jerky locomotion being caused entirely by the anterior whip.

The trailing flagellum seems broader in living than in fixed material, measuring about 3$\mu$ in some specimens. It is turned in a counterclockwise spiral. Its proximal part is applied by one edge closely to the surface of the body, and often, a short distance beyond its origin, it runs almost transversely across at a level just posterior to the nucleus. (pl. 8, fig. 60).

Interior to the proximal portion of the trailing flagellum the cresta may be seen as a clear, optically empty space in the cytosome. It is flattened, and one edge is applied to the outer edge of the body. This edge and the edge of the flagellum meet.

The undulations of the trailing flagellum are very rapid and vigorous in fresh, living specimens. In slowly moving, moribund flagellates it may be observed that undulations occur only beyond the region of the cresta or along its posterior portion, the most anterior part of the flagellum remaining inactive. Sometimes only the distal half of the flagellum undulates; sometimes, only the anterior part of the region beyond the cresta. Such movements cause a restricted vibratory movement of both the proximal part and the underlying cresta, which thereby may be shifted somewhat. It seems clear that the cresta serves as a sort of anchor for the anterior part of the trailing flagellum. It appears to be firm but flexible.

The attachment, however, is insecure. In some living but moribund flagellates, the flagellum becomes entirely detached up to its point of origin, and such detachment is usual upon fixation. The attachment is firm enough so that normally cresta and flagellum remain parallel and move together, but not so firm that it cannot very easily be broken without special mechanical effort to do so.

I have watched many crestas for long periods without observing any self-initiated movement of this organelle. Two or three abnormally formed but still living devescovinids were observed in which the end of the cresta projected beyond the limit of the body, as sometimes occurs in fixed material.

The parabasal body is distinct and sharply outlined in fresh, living material. Its diameter is about the same throughout its length. The anterior end is often bent sharply and extends across the anterior surface of the nucleus, the blepharoplast being situated near the bend. The length of this transverse anterior portion is variable. In some specimens it is almost as long as the diameter of the nucleus.

Most interesting is the rotation of the entire system of organelles in a counterclockwise direction as viewed from the rear. This has been observed so frequently that it appears to be the usual process in specimens confined under the coverglass. Whether or not it occurs in individuals in the normal environment has not been determined. The whip is carried around in a counterclockwise direction, and with it the papilla and trailing flagellum, the latter of which maintains its normal transverse bend across the body. But, instead of the entire body, only this anterior part and the differentiated organelles rotate. Evidently, in the region posterior to the papilla and cresta, the anterior cytoplasm is turned upon the posterior, which remains stationary. There must be no persistent pellicle or permanently differentiated surface layer, for this would be twisted apart. The revolution is not a continuous process. It takes place intermittently, a part turn being followed by a period of rest, then another part turn occurring, and so on. Never has rotation in the opposite direction been seen.

### **Devescovina uniflexura** sp. nov.

(Pl. 8, figs. 53–55; pl. 9, figs. 66–67; fig. C, 4)

*Type host.*—*Kalotermes perezi* Holmgren.[1] Costa Rica.

T-133. Cartago. (Syntype slides TP-73:3, 4, 17.)

*Diagnosis.*—Length 40 (32–49)μ; width 12 (9.5–15)μ; trailing flagellum a narrow ribbon, ½–1μ broad; cresta length 7 (6–7.2)μ, anteromedial edge 1½–2μ; parabasal body spiraled once or very little more, seldom having as many as 1½ turns; nucleus 3.7 (2.3–4.2) by 2.5 (2–3.1)μ; adherent rods present; no adherent spirochaetes.

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[1] The specimens of the termites were recently determined as this species by Emerson. Previously I had mistakenly referred to it (1928, 1930) as *K. marginipennis* Latreille and (1932) as *K. snyderi* Light.

The cresta (pl. 8, fig. 55; fig. C, 4) has an unusually narrow form, as compared to that of *D. hawaiensis* and other species. Not only is the anteromedial edge rather short, but the posteromedial edge curves sharply inward just posterior to its union with this so that the rest of the cresta is narrow.

The parabasal body is of the same diameter in all its parts. Its anterior end is often turned at a right angle for a short distance. The longitudinal part is not reduced in size. The parabasal body turns at a right angle near the posterior end of the nucleus and bends around it and the axostyle in a short spiral. Its posterior part is never extended straight.

Where the trunk of the axostyle meets the nuclear membrane, there is a deep-staining conical or triangular body (fig. C, 4). The membrane is separated from the central chromatin mass of the nucleus by a clear zone, and sometimes, at least, the nuclear membrane is clearly continuous anterior to the conical body. It appears to be a structure in the enlarged postnuclear part of the trunk of the axostyle, and not part of the nucleus.

There are no adherent microörganisms other than rods like those present on other species of the genus. These (pl. 8, fig. 54) are usually more or less curved and pointed at the ends, very slender, and in most preparations appear uniform in texture. The length, which varies from about 6 to 12μ, is usually about 7 or 8μ. In a few specimens it has been possible to distinguish granules arranged like those in the larger schizophytes shown by Duboscq and Grassé (1927, pl. 16, fig. 3) on *"Devescovina" hilli* and identified as *Fusiformis termitidis*. In certain preparations some of these microörganisms are clearly separated from the surface of the flagellate (pl. 9, fig. 66).

### **Devescovina hawaiensis** Janicki, emend.

(Pl. 9, figs. 62–65; fig. C, 8, 9; fig. D, 1, 2)

*Devescovina striata* A. Foà var. *hawaiensis* Janicki, 1911, *partim*, Biol. Centralbl., 31:322, figs. 1, 2.—Janicki, 1915, Zeitschr. w. Zool., 112:575, pl. 13, figs. 1–13; pl. 14, figs. 14–17.—Kirby, 1926, Univ. Calif. Publ. Zoöl., 29:105, fig. A, 2.

*Type host.*—*Neotermes connexus* Snyder. Hawaii. (Incorrectly named by Janicki *N. castaneus* Burmeister.)

T-306. (Fullaway.) (Xenosyntype slides TP-208:4, 8.)

T-305. (Bryant.) (Xenosyntype slides TP-198:33, 2, 15.)

*Diagnosis.*—Length 42 (29–65)μ; width 13 (8–28)μ; trailing flagellum a narrow band, width about 0.6–1.2μ; cresta 6.4 (5.5–8)μ, anteromedial edge 2.5–3μ, posteromedial edge bent inward sharply just before meeting anteromedial edge; parabasal body turns 1–5, majority 1½ or less; suspensorial lamella band-shaped, bent at right angle, between blepharoplast and side of nucleus; trunk of axostyle surrounded at a distance of about a fifth or more of the length from the pointed posterior end by one or two close-fitting, deep-staining rings; nucleus 5.1 (4.8–5.4) by 4.6 (3.9–5.3)μ; *Fusiformis*-like rods long and slender; no adherent spirochaetes.

Janicki studied living material and preparations from *Neotermes connexus*, as well as smears from *Cryptotermes grassii*, in Grassi's laboratory in Rome. He gave no original figures of *Devescovina striata* from the latter host, however, and apparently based his comparison in large part on Foà's description. He pointed out the following differential characteristics for the variety *hawaiensis:* somewhat larger size, presence of broad forms, parabasal body with more turns in the broad forms. These characteristics, considered by themselves alone, would not be enough for specific separation. But the characteristics of the crestas and trailing flagella seem clearly to warrant specific distinction, and, consequently, Janicki's variety is raised to species status.

Janicki recognized only the one species *D. hawaiensis* in the Hawaiian termite, but I have separated from it a new species, *D. exilis,* for reasons given in the account of that flagellate (p. 50). It is not possible to distinguish the two species in Janicki's account, but the broader forms with the greater number of turns of the parabasal body are the ones he emphasized as characteristic of *D. hawaiensis.* The name, therefore, is retained for this part of his species.

Janicki noted the occurrence of two forms: an abundant, slender, posteriorly pointed one, and a less frequent broad one. The first form, which is very much more abundant than the other, includes the usual forms of *Devescovina hawaiensis* and all forms of *D. exilis;* the second form is entirely *D. hawaiensis.* In the broad form, also, the posterior end is normally pointed, not broadly rounded as Janicki represented it in his plate 13, figures 2 and 3, but on smear preparations the shape is often abnormal. The broad form may have a breadth of 25$\mu$, as Janicki stated, but the length including the caudal extension is more than twice this. Broad forms are infrequent in some material, more numerous in other material. Except for turns of the parabasal body in the stout one, the structure of the two forms is identical.

Janicki described the blepharoplast as a relatively large body consisting of a membrane within which are several granules. In some of his figures its diameter equals the thickness of the parabasal body. The blepharoplast group is much smaller than this, however; it is an aggregate of four or five granules closely packed together and has an uneven outline with no surrounding membrane.

In Janicki's figures the cresta is represented as smaller than it actually is and its true shape is not given. I have never observed it to be a straight-sided triangle. There is a characteristic sharp bend inward of the posteromedial edge soon after it leaves the anteromedial edge (fig. C, 8; pl. 9, fig. 63). The posteromedial edge has a length always amounting to twice or more that of the anteromedial edge.

Janicki observed the form of the parabasal body correctly, but the many turns shown in certain of his figures, one of which is often reproduced as representative of the genus, are not typical. I have never seen a specimen with more than 5 turns, and among thousands of specimens only one with so many. Of 50 individuals, two-thirds had parabasals with 1½ turns or fewer. Larger ones usually have 2 or 3 turns, and very few have more. The first turn is characteristically broad and open, with the terminal part sometimes extended outward somewhat. When there are 2 or 3 turns, the spiral is closer, and successive turns are usually close together. Janicki stated that in the broad form there are 3 to 8 parabasal turns; but 8 turns must be rare. The figures Janicki made of the broad forms (his pl. 13, figs. 2 and 3) have parabasals with about 6 and 5 turns, respectively, and in both the spiral appears to turn in the wrong direction.

Janicki stated that the parabasal filament runs the length of the parabasal body on the side facing the median axis, and showed it passing to the blepharoplast from the anterior end of the structure. In the spiral the chromophile element usually appears as a band. It separates from the other substance about halfway along the longitudinal part, and runs as a filament separately to the blepharoplast, close along the anteromedial edge of the cresta (fig. C, 9). This anterior filament was not represented by Janicki, and apparently he did not see the actual connection to the blepharoplast. I have observed the nuclear rhizoplast in the position of Janicki's parabasal filament; possibly Janicki was actually describing the rhizoplast.

The structure termed by Janicki (1915) the suspensorial lamella I have observed only in *Devescovina hawaiensis*. It is a narrow lamella (pl. 9, fig. 63; fig. C, 8) passing ventrally from the blepharoplast for a short distance along the bases of the anterior flagella, then turning posteriorly. Its posterior end usually lies against the nuclear membrane near the middle of the ventral side. As seen from the edge, it appears to be a moderately stout filament, as Janicki (1911) believed it to be when he labeled it "Suspensorialfaden." From other aspects it is a band, rounded or truncate at its posterior end, even in diameter to the bend for a short distance ventral to the blepharoplast, where it turns sharply dorsally and narrows to its anterior end. It has not been determined whether the lamella meets the blepharoplast directly; it seems not to, rather passing close to it. The posterior portion of the lamella may be applied to the nuclear membrane, sometimes flat, but at least some few times by one edge. The staining properties of the suspensorial lamella differentiate it from the cresta and parabasal body. It does not take iron-haematoxylin so readily as does the cresta, and is, in fact, not often well demonstrated. It was seen clearly in only one set of smears, which were counterstained with erythrosin after iron-haematoxylin. It does not stain with Delafield's haematoxylin, whereas the parabasal body stains deeply. The suspensorial lamella clearly is a separate structure, not part of the capitulum of the axostyle.

The dorsal edge of the capitulum of the axostyle appears as a slender filament passing along the nuclear membrane to a position near the blepharoplast. The anterior edge runs parallel to the roots of the anterior flagella nearly to the tip of the papilla (fig. C, 8). It then turns sharply and continues, appearing as a heavy-staining, narrow lamella, nearly to the posterior end of the nucleus. No membranous structure can be seen; my opinion that it is a part of the capitulum is based on interpretation and comparison.

The trunk of the axostyle is moderately stout, contains a haematoxylin-staining conical core just posterior to the nucleus (pl. 9, fig. 63), and tapers posteriorly, within the cytoplasm, to a filament (pl. 9, fig. 62). It does not become reduced to a filament so soon as in some other species of *Devescovina*. In its posterior part, before it becomes a filament and while it is still at some distance from the terminus of the body, it is surrounded by one or two small, close-fitting, iron-haematoxylin-staining rings (pl. 9, fig. 62). The presence and position of these is a constant characteristic of *Devescovina hawaiensis*. In specimens with a rounded posterior end the posterior part of the axostyle is turned back under the surface. In some pointed individuals, however, the filamentous terminal part of the axostyle likewise is recurved (pl. 9, fig. 62).

Janicki considered the *Fusiformis*-like microörganisms to be pellicular striations, but he noted their discontinuity, their variability in direction and grouping, and their occasional separation in living animals as fine, irregularly arranged rods. These observations might have suggested their true nature, which Duboscq and Grassé pointed out in *Polymastix, Lophomonas striata,* and *"Devescovina" hilli,* though they made no observations on a true *Devescovina.* The microörganisms on *D. hawaiensis* are of the long, slender type, close-set, and mostly longitudinal in direction. As Janicki noted, they are not present on the most anterior part, but cover the body elsewhere.

Wood fragments are generally abundant (fig. D, 2), especially in larger individuals, the bodies of which are often densely packed with them. Janicki's figures do not show the normal situation in this respect, although he described the occurrence of wood. He did not observe ingestion, but he believed that there is no mouth and that the whole body surface may participate in food ingestion.

### **Devescovina transita** sp. nov.

(Pl. 3, fig. 28; fig. C, 10–13)

*Type host.*—*Glyptotermes* sp. nov. Java.
T-4571. Bandjar. (Syntype slides TP-3233:6, 10.)
T-4567, 4559. Bandjar. (Xenosyntype slides TP-3229:8; 3248:3.)
*Additional hosts*—
*Cryptotermes cynocephalus* Light. Java.
T-4537. Buitenzorg. (Homosyntype slide TP-3224:10.)
T-328. (Cleveland. Collier.) (Homosyntype slide TP-256:1.)
*Glyptotermes dilatatus* (Bugnion and Popoff). Ceylon.
T-318. (Cleveland. Collier.) Paradeniya. (Homosyntype slide TP-263:6.)
*Kalotermes repandus* Hill. Fiji Islands.
T-516. (Hill 4064.) (Homosyntype slides TP-516:3, 5.)

*Diagnosis.*—(From type host): length 44 (38–52)µ; width 19 (11–26)µ; trailing flagellum a narrow band, usually less than 1µ wide; cresta 8.2 (6.5–9.5)µ, anteromedial edge 2–2.5µ; parabasal turns close together, 3¾ (1½–5½), exceptionally as much as 7; nucleus 4.5–6 by 4–5µ; *Fusiformis*-like microörganisms typical; no adherent spirochaetes. (From *Cryptotermes cynocephalus* T-4537): length 46 (38–60)µ; width 17 (12–28)µ; trailing flagellum variable, cord to band about 1µ wide; cresta 7.3 (6–8)µ, anteromedial edge 2–2.5µ; parabasal turns close, 2 (1–3½); nucleus 3.5–6 by 2.5–4.5µ; no adherent spirochaetes. (From *Glyptotermes dilatatus*): length 35 (21–46)µ; width 17 (12–25)µ; trailing flagellum a cord or narrow band; cresta 6 (4.8–6.9)µ; parabasal turns close; tuft of spirochaetes on anterior portion. (From *Kalotermes repandus*): length 38 (30–47)µ; width 17 (11–26)µ; trailing flagellum a cord or narrow band; cresta 6 (5.3–6.7)µ; parabasal turns close, 2¾–3½; nucleus 5.7 (4.7–6.7) by 4µ. No adherent spirochaetes.

This species is a particularly difficult one to place. Some specimens resemble certain individuals of *D. lemniscata,* but in general the narrower trailing flagellum is a distinction from that species; others resemble some specimens of *D. glabra.* The trailing flagellum more often develops into a narrow band than in *glabra,* and in many specimens of *glabra* the parabasal spiral is somewhat drawn out, successive turns being separated by about its thickness, whereas in *D. transita* successive turns are close together. Taxonomically, *D.*

*transita* is the least satisfactory species of *Devescovina.* It appears not to be a naturally uniform species, and it may well be that it is actually merely a group of variants of other species or is composed of flagellates of unlike origin. The inclusion in it of forms with a certain group of characteristics is an expedient, rather than an expression of phylogenetic relationships.

No chromatic shield has been seen in any specimens, and it seems likely that this is definitely absent from *D. transita* of *K. repandus.* On slides bearing the latter species, *D. cometoides* was also present, and showed the chromatic shield very clearly.

### **Devescovina similis** sp nov.

(Fig. C, 7)

*Type host.*—*Cryptotermes* sp. nov. Madagascar.

T-4459. Manantantely, near Fort Dauphin. (Syntype slides TP-3168:10, 3.)

*Diagnosis.*—Length 47 (38–58)μ; width 10 (8.5–12.5)μ; trailing flagellum a narrow band, maximum width about 1μ; cresta length 6.1 (5.3–7)μ; anteromedial edge 2–2.5μ; parabasal spiral close, turned 2 (1¼–2½) times; chromatic shield present; nucleus with no space between membrane and chromatin mass, size 5–5.8 by 3.3–4.1μ, averaging 5.3 by 3.4μ; surface bearing long, slender, adherent microörganisms; spirochaetes on anterior end only.

The parabasal body is wound in a tight, close spiral. The chromophile element in the spiral is a band, which narrows posteriorly. It separates as a filament near the anterior end of the nucleus, more anteriorly than in some species, and passes direct to the blepharoplast. The other substance of the parabasal is enlarged at the anterior end; there is apparently no hook.

A well-defined chromatic shield exactly like the one in *D. cometoides* is present in this species.

The nucleus in the material examined had no space under the membrane, and it was rather light-staining. There are a few scattered, deep-staining granules, besides the nucleolus, but the nucleus has no deep-staining mass such as occurs in many species of *Devescovina,* and no abundance of granules as in *D. coghilli.*

The flagellate resembles *D. transita* in many respects, but it is much slenderer, has few parabasal turns, and, as has already been stated, it has the chromatic shield, which seems to be absent from *D. transita.*

## SUMMARY

This publication is the first part of a treatise on the polymastigote flagellates of the subfamily Devescovininae, all of which occur in termites. There is a general account of devescovinid flagellates and of the genus *Devescovina,* followed by a key to the species and a description of each of them. Included in the genus are twenty species, of which fourteen are new; one previously described species is emended, and several originally assigned to *Devescovina* have been removed from the genus. Summaries of the characteristics of the subfamily and the genus are given in the respective diagnoses (pp. 6, 16).

A discussion is given of the opinion of some authors that markedly different forms occur as different stages in the life cycle of devescovinids, and of the consequent inclusion, in the supposed developmental cycle of one species, of

flagellates that in my opinion belong to different species and genera. The interpretation is rejected, and the practice is adopted of treating forms markedly different morphologically as different species of these asexually reproducing flagellates.

Of particular interest in the morphology of *Devescovina* is the ribbonlike form, reaching 3$\mu$ in breadth, developed in some species by part of the trailing flagellum. Among devescovinids that feature of development is most evident in this genus.

The parabasal body, which in all members of the genus is turned in a laeotropic spiral around the anterior part of the axostyle, is generally simple. A branched condition, in which there is only one ramus, is characteristic of one species, *D. fissa;* it also occurs in occasional specimens of some other species.

The axostyle is also of a simple type. It is generally reduced to a filamentous posterior part which is entirely enclosed in the cytoplasm; and the capitulum, except in *D. insolita,* remains a simple anterior expansion.

Wood is ingested, presumably through the surface of the posterior part of the body, by all except one species. Usually the particles are distributed evenly in the cytoplasm posterior to the nucleus; but in two species, *D. tendicula* and *D. vittata,* there is often a localization of wood in the part nearest the parabasal body.

Rod-shaped microörganisms, of the type of *Fusiformis* described on polymastigote flagellates by Grassé, adhere to the surface of all species, resulting in apparent striations. Usually they are present on all parts of the body except the extreme anterior; but in two species, *D. robusta* and *D. insolita,* they are restricted to the posterior part.

Adherent spirochaetes, either restricted to a definite area in the region of the papilla or distributed more widely on the body surface, are usually or always present on some species and uniformly absent from others. There is an exceptional occurrence of adherent spirochaetes on a species in a certain host.

A dense aggregate of granules or short rods, forming a ring around the anterior part of the trunk of the axostyle, is constant in certain material of *D. glabra* and *D. lemniscata.* These bodies are evidently microörganisms comparable to those similarly aggregated in *Joenia annectens.*

In living devescovinids, as observed especially in *Devescovina lemniscata,* the three anterior flagella are united for part or all of their length into a whip. Movements of this are accompanied by lateral movements of the papilla. The trailing flagellum is undulatory and is insecurely adherent to the surface above the cresta. Jerky progressive locomotion may be produced by activity of all the flagella, or of either type alone. No self-initiated movement of the cresta has been seen in *Devescovina.* Under certain circumstances there is an intermittent rotation of the entire system of organelles, together with the papillar region of the body, whereas the rest of the cytoplasm remains stationary. The anterior part of the cytosome, including the surface layer, thus turns upon the posterior part. Rotation has been observed in one direction only, counterclockwise as viewed from the posterior end of the body.

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# PLATES

All figures drawn with the aid of the camera lucida. Abbreviations for methods of preparation: B., Bouin's fluid; C., Champy's fluid; D., Delafield's haematoxylin; E., eosin; Er., erythrosin; F., acid fuchsin; Fl., Flemming's fluid; H., iron-haematoxylin; Holl., Hollande's fluid; Os.V., osmic vapor; R., Regaud's haematoxylin; S., Schaudinn's fluid.

## PLATE 1

Figs. 1–4. *Devescovina elongata* Bernstein from *Anacanthotermes ochraceus.*

Fig. 1. Rod-shaped bacteria adherent to surface; some show evidence of binary fission. S.H.

Fig. 2. General structure, showing full length of flagella and characteristic form of papilla. S.H.

Fig. 3. Adherent spirochaetes, which are present on almost all specimens but are omitted from the other figures. S.H.F.

Fig. 4. Blepharoplast, origin of flagella, cresta, nucleus with nucleolus, and parabasal body. S.H.

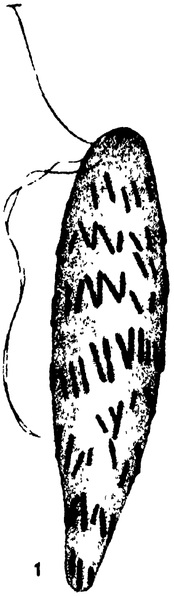
Figs. 5–7. *Devescovina cometoides* de Mello and de Brito.

Fig. 5. From *Cryptotermes dudleyi.* External aspect, full length of cordlike trailing flagellum, longitudinal rods adherent to surface, spirochaetes in tuft on region of papilla and distributed elsewhere on the body. S.H.E. × 1400.

Fig. 6. From *Cryptotermes* sp. T-329, Java. General cytology, full length of flagella, partly double aspect of parabasal body. C.R.

Fig. 7. From *Cryptotermes dudleyi.* Detail; capitulum of axostyle. S.H.E.

Scale A, figs. 1–4, 6, 7, × 2400.



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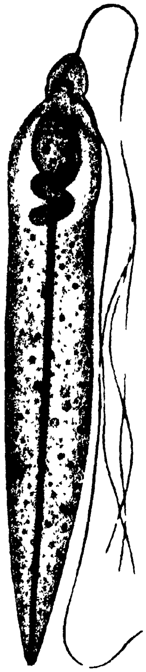

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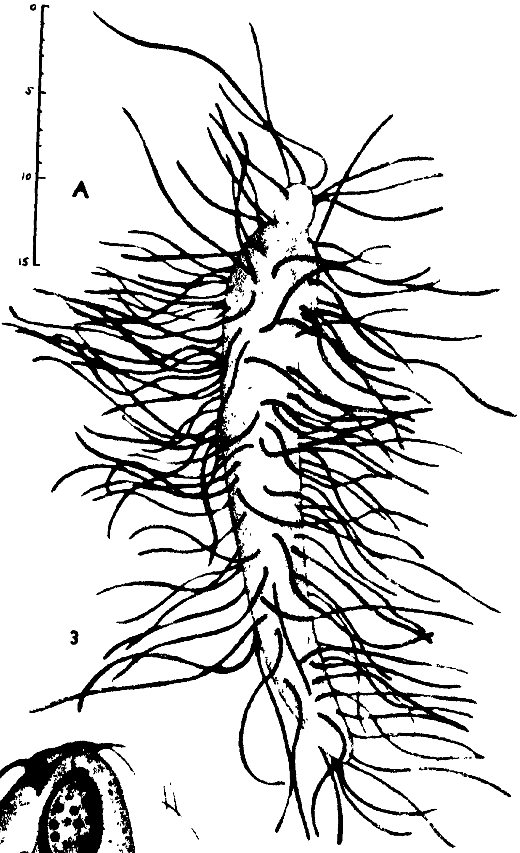

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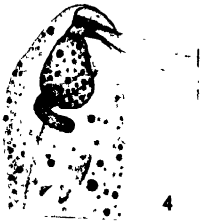

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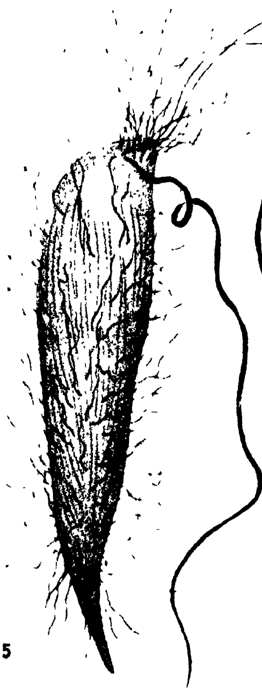

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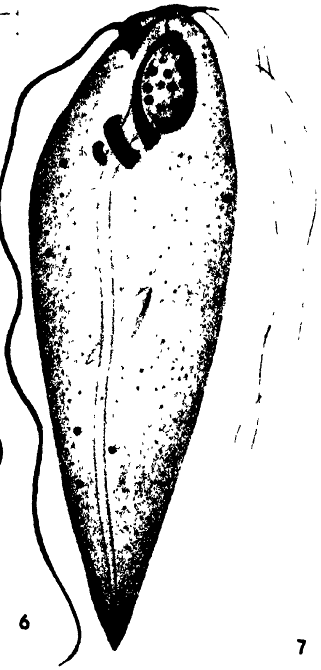

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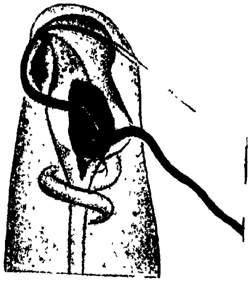

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## PLATE 2

Figs. 8–11. *Devescovina cometoides* de Mello and de Brito.

Fig. 8. From *Glyptotermes dilatatus.* Tuft of spirochaetes adherent to papilla. S.H.

Fig. 9. From *Kalotermes* sp., Damaum (type host; slide sent by de Mello).

Figs. 10–11. From *Cryptotermes dudleyi.* 10. Entire, sinuous axostyle. S.H.E. 11. Parabasal body, characteristic form tapered posteriorly. S.D. × 2400.

Figs. 12–14. *Devescovina glabra* Grassi.

Fig. 12. From *Cryptotermes havilandi.* Entire.

Fig. 13. From same host. Detail showing cresta. × 2400.

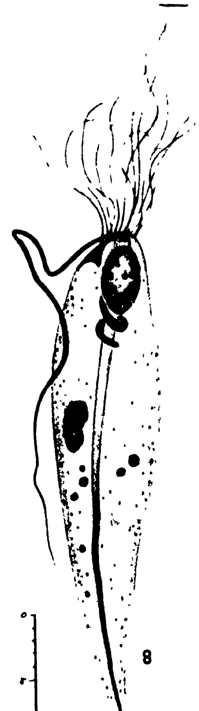
Fig. 14. From *Neotermes zuluensis.* Parabasal body with a branch at the beginning of the coiled part. S.D. × 2330.

Figs. 15–21. *Devescovina fissa* sp. nov. from *Procryptotermes* sp. nov., Réunion.

Figs. 15–19. Different views of parabasal body, showing the branch arising at the beginning of the spiral, present in the majority of specimens. Usually, as in 17 and 18, it joins the parabasal substance again. S.D.

Figs. 20–21. Views of opposite sides of the anterior part, showing cresta, nucleus, granules of chromatic shield. S.H. × 2330.

Scale B, figs. 8, 9, 10, 12, × 1770.



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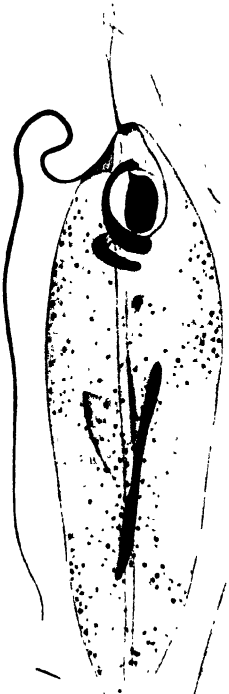

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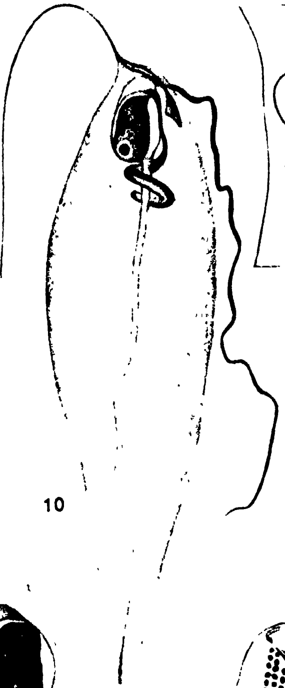

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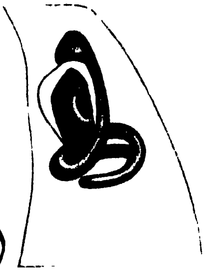

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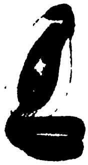

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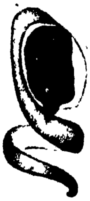

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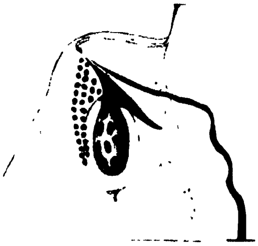

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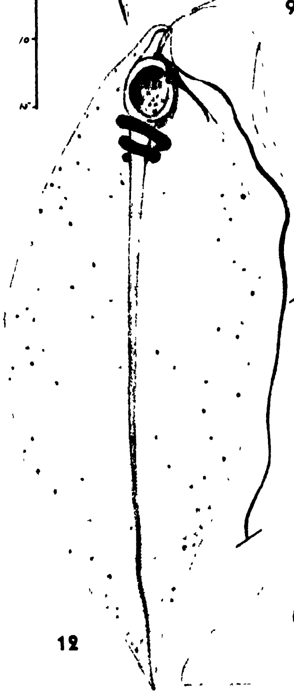

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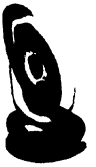

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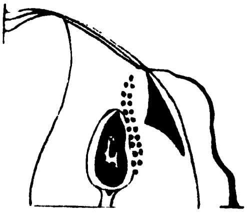

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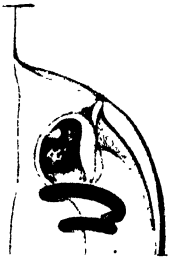

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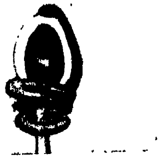

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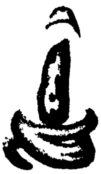

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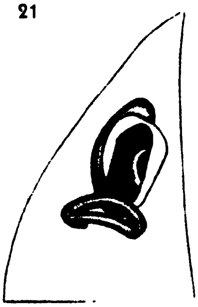


17

## PLATE 3

**Figs. 22–24. *Devescovina tendicula* sp. nov. from *Kalotermes jeannelanus.***

**Fig. 22. Entire, spirochaetes and rods omitted. Fl. H. × 1700.**

**Fig. 23. Parabasal body, with characteristic sigmoid curve in the longitudinal part, broad loop, filament separating anteriorly to pass to blepharoplast; cresta. Fl. R. × 1700.**

**Fig. 24. Anterior detail, showing chromatic shield. S.H. × 1700.**

**Fig. 25. *Devescovina robusta* sp. nov. from *Neotermes erythraeus.* Spirochaetes omitted, rod-shaped bacteria adherent only to the posterior part of the body.**

**Figs. 26–27. *Devescovina insolita* sp. nov. from *Neotermes* sp. T-2012, Tanganyika**

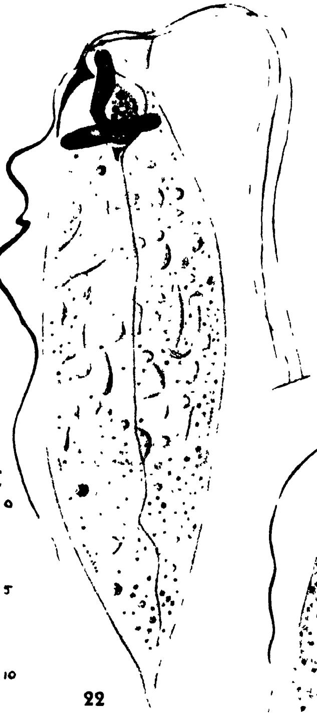
**Fig. 26. Entire, spirochaetes and rods omitted, edges of expanded capitulum of axostyle shown anterior to nucleus. S.H.**

**Fig. 27. Anterior part, capitulum of axostyle. S.H.**

**Fig. 28. *Devescovina transita* sp. nov. from *Glyptotermes dilatatus.* Small form. S.H.**

**Fig. 29. *Devescovina parasoma* sp. nov., from *Neotermes tectonae.* Cresta and parabasal body, with parabasal filament. C.R.**

**Scale C, figs. 27, 29, × 2400.**
**Scale D, figs. 25, 26, 28, × 1770.**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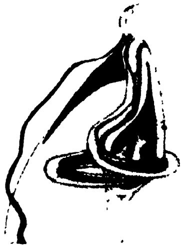
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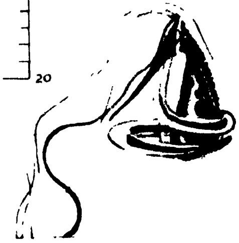
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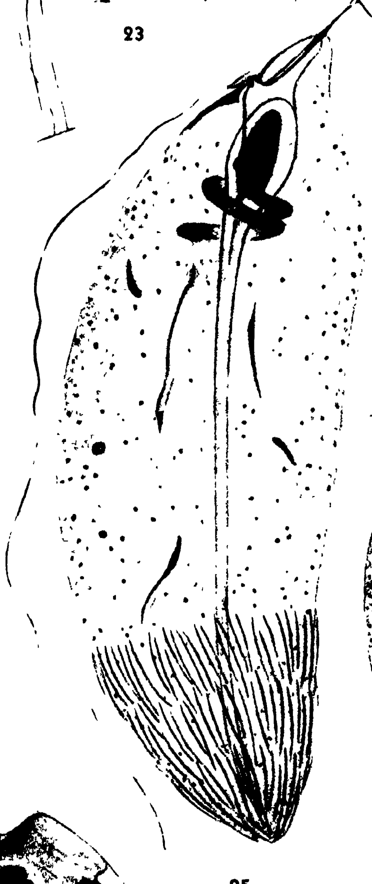
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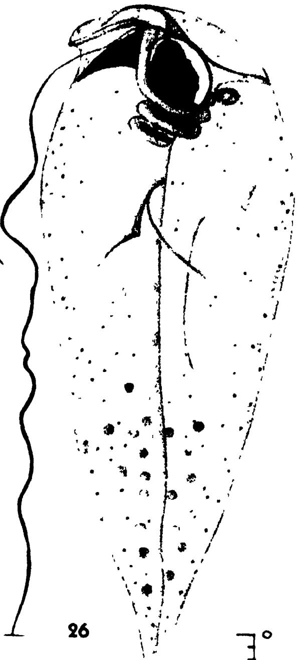
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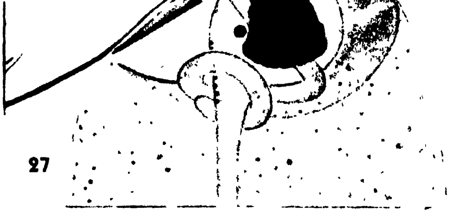
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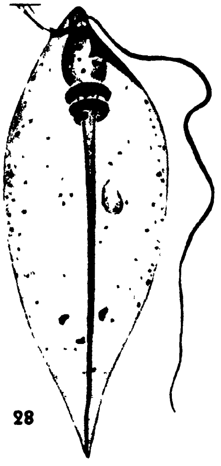
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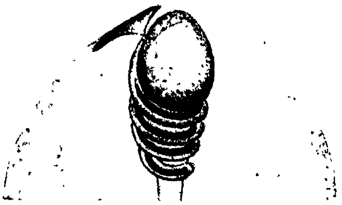

29

## PLATE 4

Figs. 30–32. *Devescovina parasoma* sp. nov. from *Neotermes tectonae.*

**Fig. 30.** External aspect, showing adherent spirochaetes, slender rods on surface, and stouter rods adherent by one end to the posterior part. S.H.

**Fig. 31.** Cresta, parabasal body, and nucleus. C.R. × 2400.

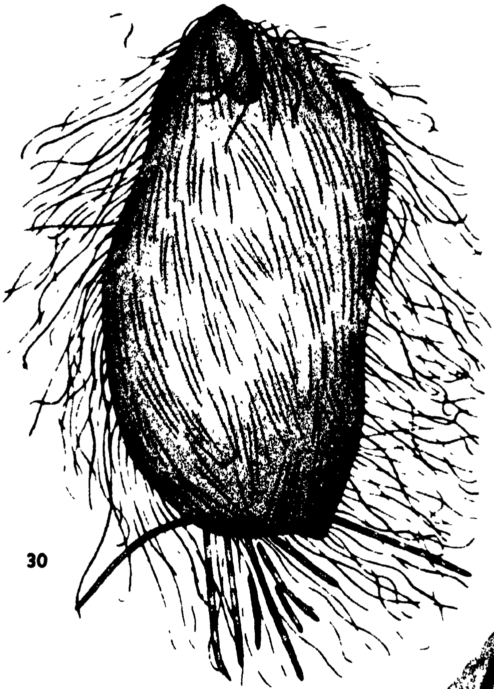
**Fig. 32.** Cytological detail; trailing flagellum somewhat flattened; trunk of axostyle moderately stout, and projecting from cytoplasm. S.H.

Figs. 33–35. *Devescovina vestita* sp. nov. from *Glyptotermes niger.*

**Fig. 33.** Parabasal body. Fl. R. × 2334.

**Figs. 34–35.** Detail from opposite sides of body; parabasal body extended beyond blepharoplast on the anterior surface of the nucleus, chromophile element band-shaped in spiral and separating near middle of longitudinal part to pass separately to blepharoplast; nuclear rhizoplast passing to nuclear membrane near anterior end of parabasal; typical form of cresta; spirochaetes and adherent rods omitted. Holl. H. × 3467.

Scale E, fig. 32, × 1770.
Scale F, fig. 30, × 1400.



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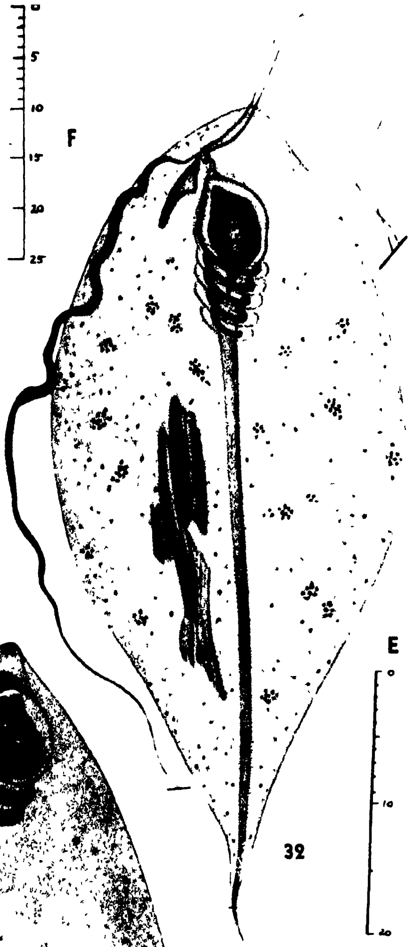

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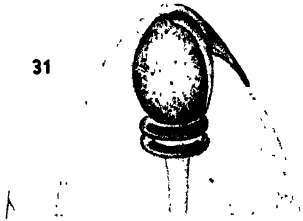

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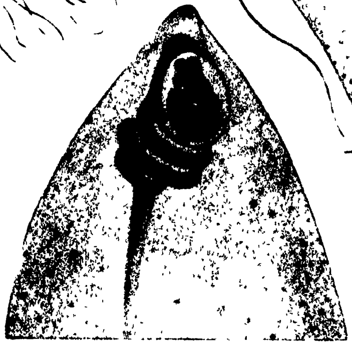

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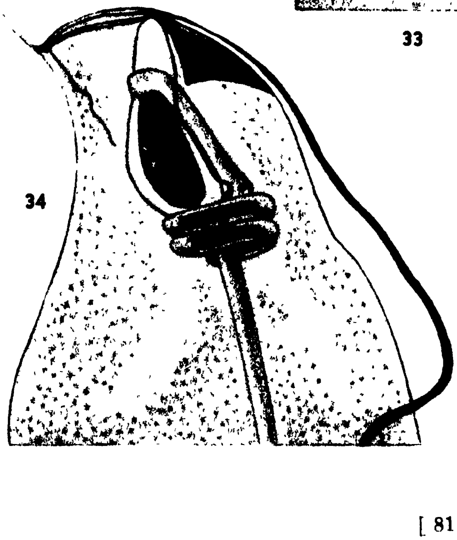

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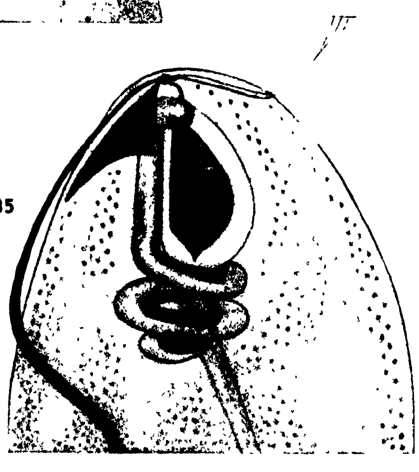

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## PLATE 5

Figs. 36–38. ***Devescovina vestita*** **sp. nov. from** ***Glyptotermes niger.***

Fig. 36. Adherent spirochaetes; trunk of axostyle relatively stout and projecting from cytosome; rods omitted. Holl. H.

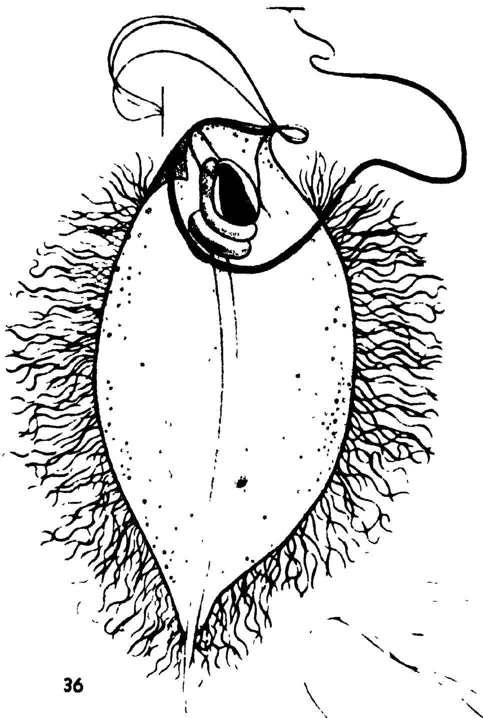
Fig. 37. Rods, shorter and stouter than in most species of *Devescovina*, adherent to surface; spirochaetes omitted. Fl. R.

Fig. 38. Four oxymonads enclosed in the cytoplasm. S.H.

Fig. 39. *Devescovina exilis* sp. nov. from *Neotermes connexus.* Spirochaetes and rods omitted. × 2400.

Fig. 40. *Devescovina arta* sp. nov. from *Glyptotermes minutus.* S. H. × 2400.

Scale G, figs. 36, 37, 38, × 2330.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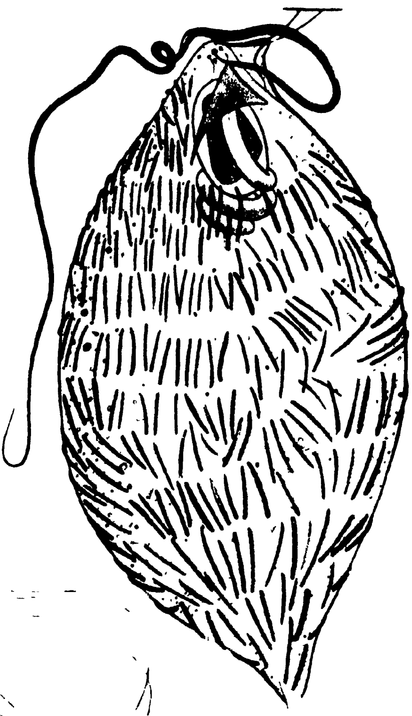
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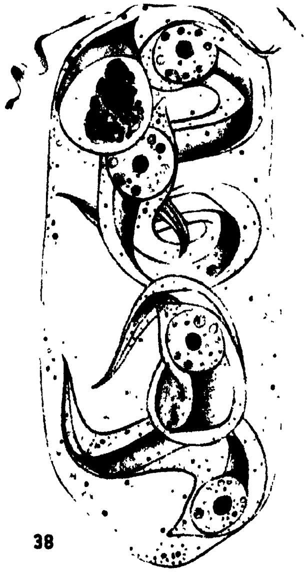
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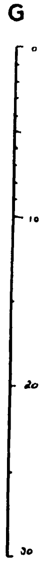
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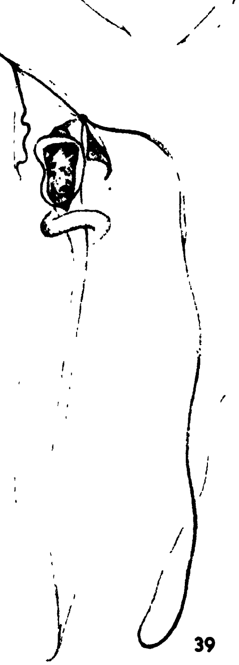
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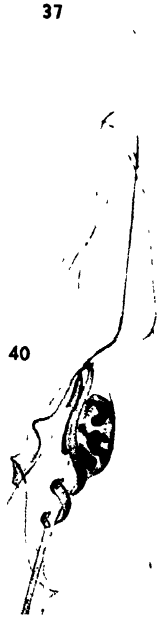
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## PLATE 6

**Figs. 41–42. *Devescovina arta* sp. nov. from *Glyptotermes angustus*.**

**Fig. 41. Entire; narrow form; bandlike trailing flagellum; slender, posteriorly sinuous trunk of axostyle; rods and spirochaetes omitted. S.H.**

**Fig. 42. Semidiagrammatic.** Nuclear rhizoplast; slender anterior part of parabasal characteristic of this species; platelike chromophile element in spiral of parabasal, shown in optical section; characteristic shape of cresta. S.H. × 3600.

**Fig. 43.** ***Devescovina arta*** sp. nov. from *Glyptotermes minutus*. Trailing flagellum entirely enclosed in cytoplasm. S.H.

Figs. 44–47. ***Devescovina lepida*** sp. nov.

**Fig. 44.** From ***Cryptotermes longicollis***. Parabasal body. S.D.

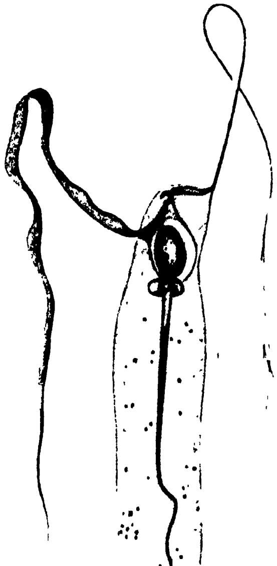
Figs. 45–47. From *Calcaritermes brevicollis*.

**Fig. 45.** Entire, rods omitted; remnant of paradesmose (?) spiraled around trunk of axostyle. S.H.

**Fig. 46.** Parabasal body drawn as though cut away in front, showing the characteristic granules that are enclosed within the spiral. S.D.F.

**Fig. 47. Parabasal body.** S.D.F.

Scale H, figs. 41, 45, × 1700.
Scale I, figs. 43, 44, 46, 47, × 2400.



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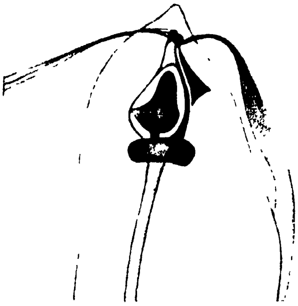

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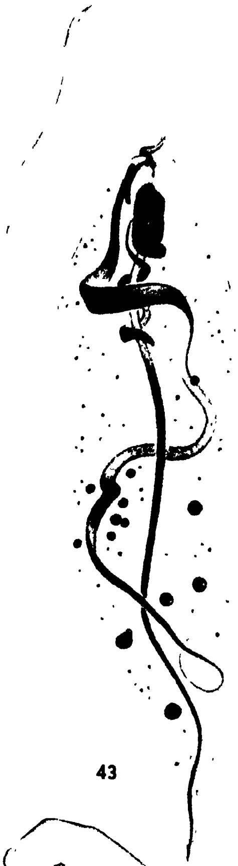

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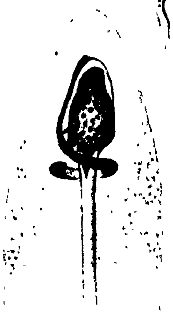

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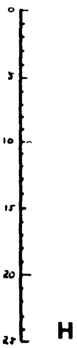

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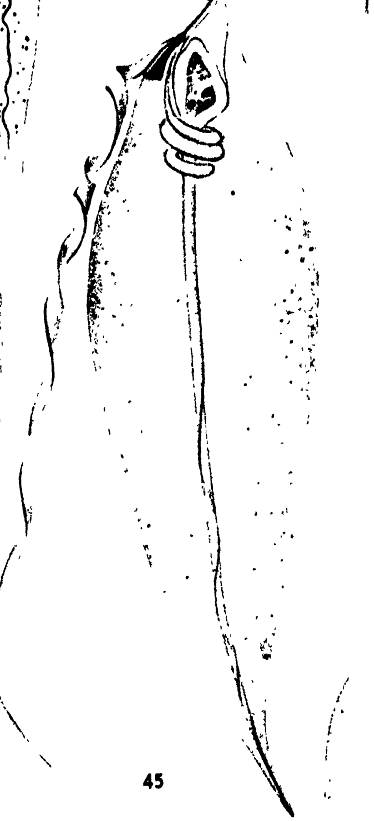

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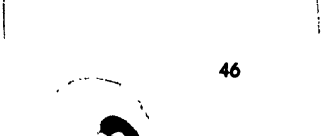

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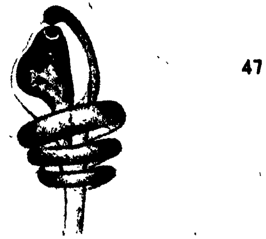


47

## PLATE 7

Fig. 48. *Devescovina lepida* sp. nov. from *Cryptotermes longicollis*. S.H.F.

Figs. 49–51. *Devescovina striata* Foà.

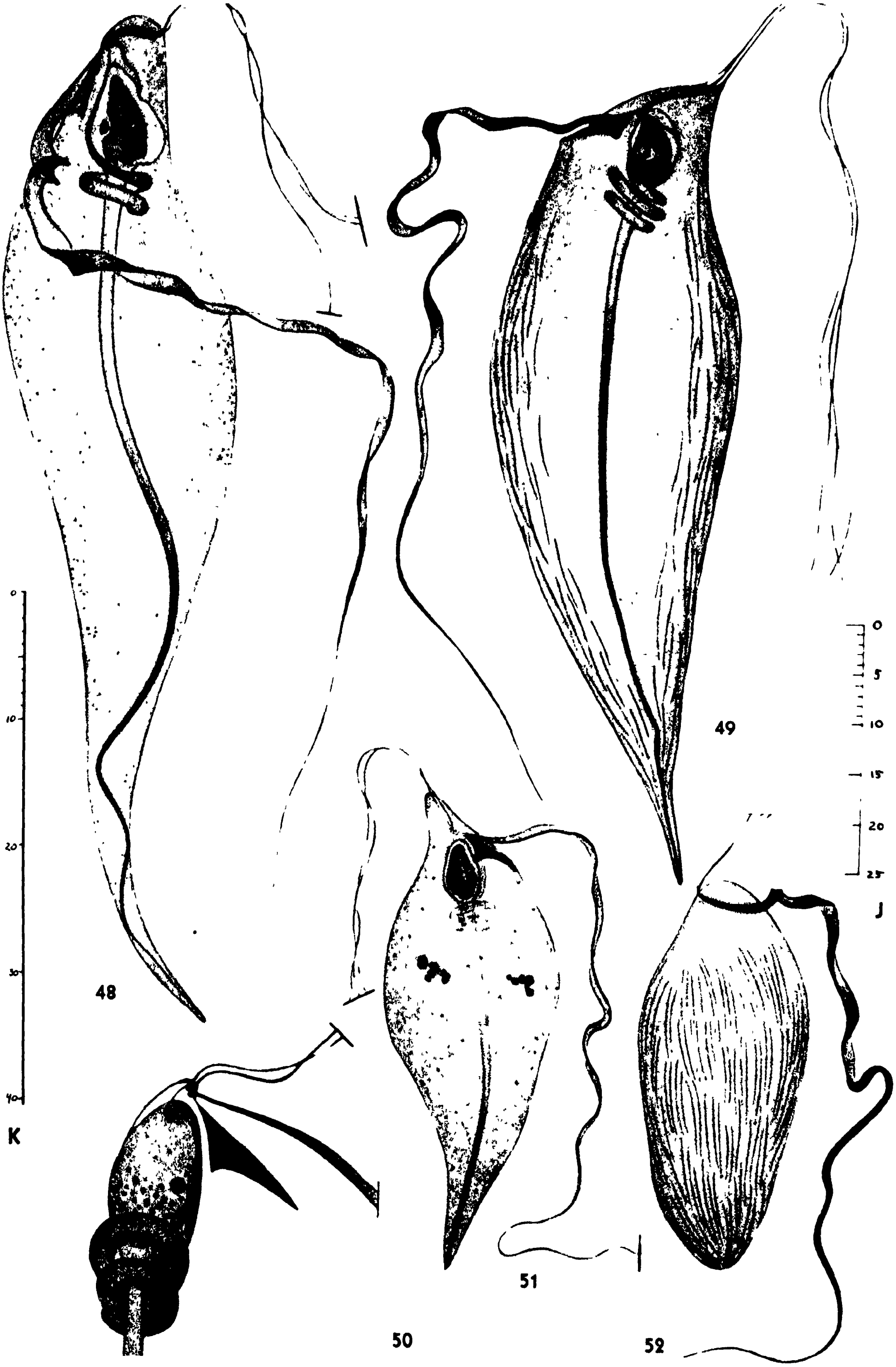
Fig. 49. From *Cryptotermes brevis*. Rods shown only at the sides; they are present on the entire surface except the papilla. Flagella shown full length. S.H.F.

Fig. 50. From *Cryptotermes piceatus*. Parabasal body; attachment of parabasal filament to blepharoplast not shown (see fig. C, 6); blepharoplast group of several distinct granules; nuclear rhizoplast; the filament to the left of the rhizoplast is probably part of the capitulum of the axostyle. B.H. Er. × 3600.

Fig. 51. From *Cryptotermes grassii*, small specimen; small size is characteristic of the specimens examined from this host.

Fig. 52. *Devescovina lemniscata* Kirby from *Cryptotermes dudleyi*. External aspect, showing externally adherent rod-shaped bacteria. S.H.E.

Scale J, fig. 52, × 1400.
Scale K, figs. 48, 49, 51, × 1770.


K
J

## PLATE 8

Figs. 53–55. *Devescovina uniflexura* sp. nov. from *Kalotermes perezi.*

Fig. 53. Papilla extended forward; expanded anterior end of parabasal body. S.D.

Fig. 54. Detail of the rod-shaped bacteria adherent to the surface. Os. H.

Fig. 55. Cresta, nucleus, blepharoplast group of several granules. S.H.E.

Figs. 56–59. *Devescovina lemniscata* Kirby from *Cryptotermes dudleyi.*

Fig. 56. Cresta raised from surface of body. S.H.E.

Fig. 57. Capitulum of axostyle; conical chromatic structure in anterior part of trunk of axostyle. S.H.E.

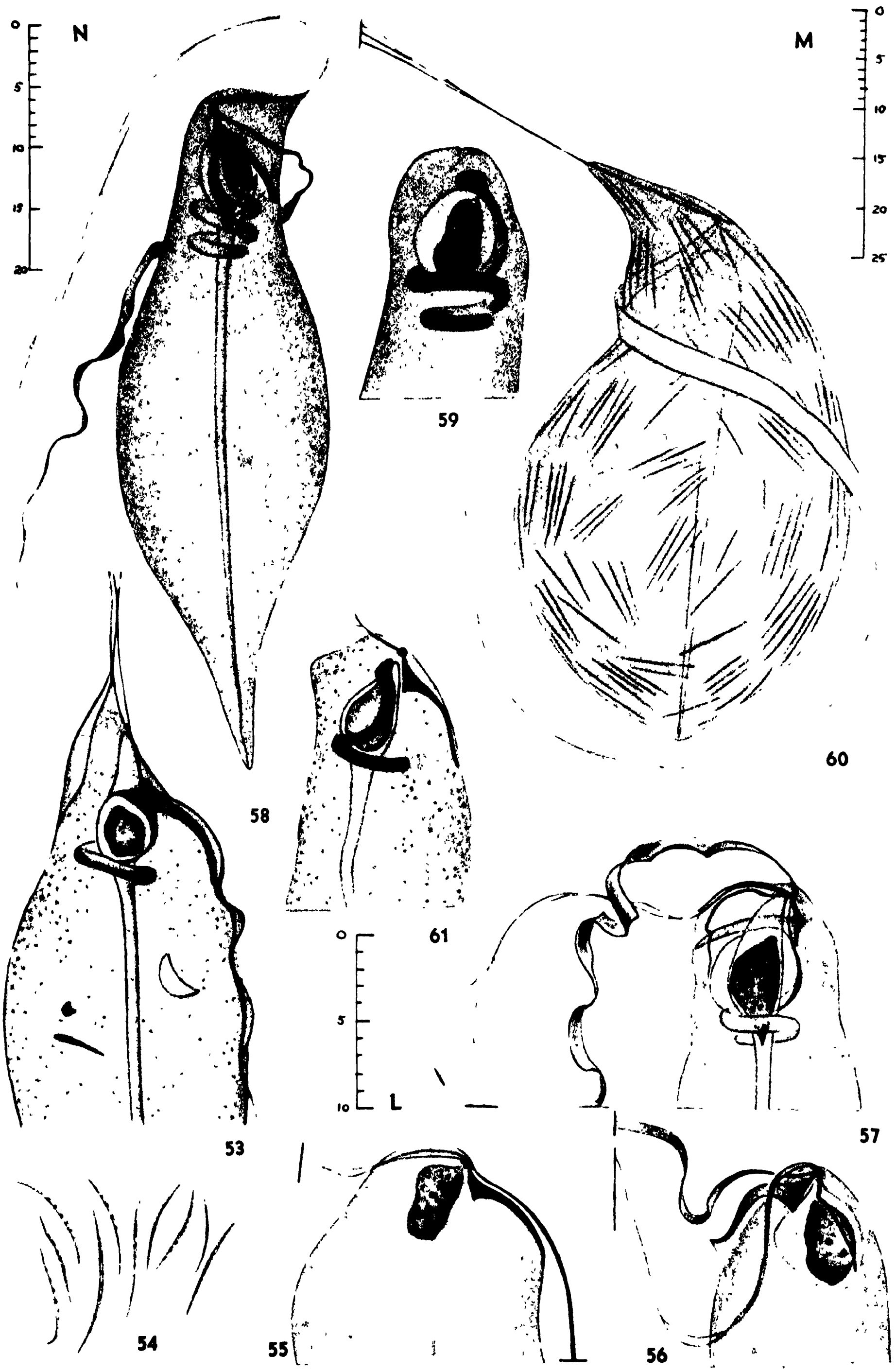
Fig. 58. Figure representative of species, rods omitted. S.H.E.

Fig. 59. Parabasal body with enlargement at anterior end. S.D.

Fig. 60. *Devescovina lemniscata* from *Neotermes insularis.* Drawing made from a living specimen, showing the natural position of the flagella, rods adherent to the surface.

Fig. 61. *Devescovina lemniscata* from *Cryptotermes hermsi,* showing the stout anterior part of the parabasal body, which was incorrectly represented in the original description. S.D.

Scale L, figs. 53–57, 59, 61, × 2400.
Scale M, fig. 60, × 1400.
Scale N, fig. 58, × 1770.


N
M
L

# PLATE 9

Figs. 62–65. *Devescovina hawaiensis* Janicki from *Neotermes connexus.*

Fig. 62. Adherent rods omitted; anterior to and beside the nucleus is the suspensorial lamella, seen on the flat side; around the posterior part of the trunk of the axostyle are the two characteristic rings. B.H.Er.

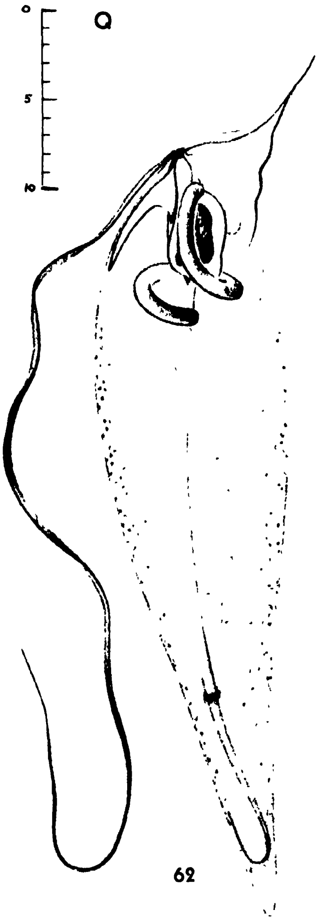
Figs. 63–65. Details of anterior structures; in fig. 64 the papilla is not visible; variations in length of spiral of parabasal body. B.H.Er.

Figs. 66–67. *Devescovina uniflexura* sp. nov. from *Kalotermes perezi.*

Fig. 66. Rods adherent to surface; some of them have become partly or entirely detached. Os. V.H.

Fig. 67. Structural detail; blepharoplast group of 4 granules; narrow cresta characteristic of this species. S.H.

Scale O, figs. 66, 67, × 1770.
Scales P, Q, figs. 62–65, × 2400.



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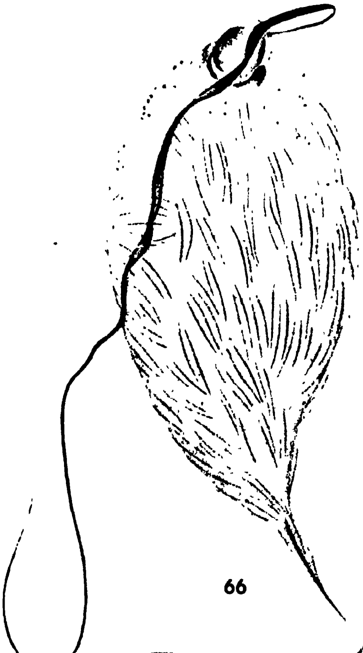

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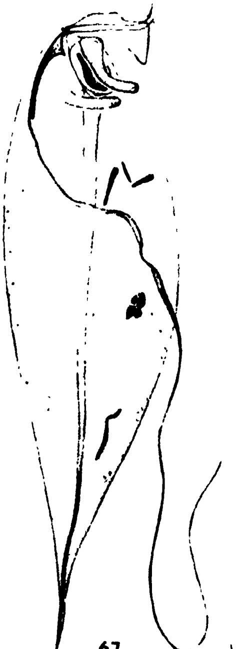

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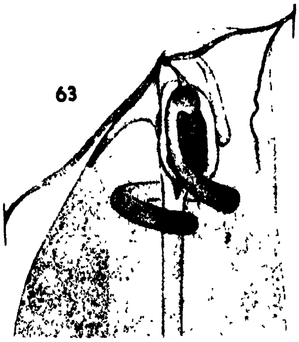

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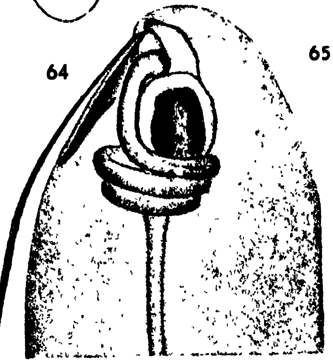

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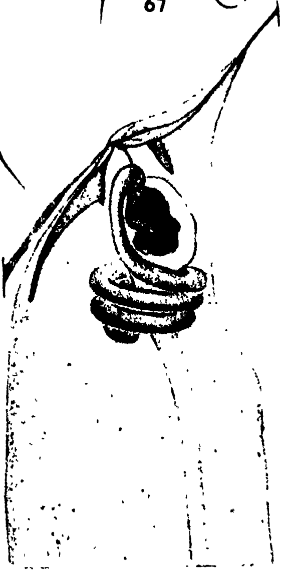

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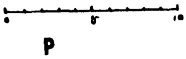

# DEVESCOVINID FLAGELLATES OF TERMITES

# II. THE GENERA CADUCEIA AND MACROTRICHOMONAS

BY

HAROLD KIRBY

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# DEVESCOVINID FLAGELLATES OF TERMITES
# II. THE GENERA CADUCEIA AND MACROTRICHOMONAS

BY

HAROLD KIRBY

## DESCRIPTIVE AND SYSTEMATIC ACCOUNT

### GENUS CADUCEIA FRANÇA

### **Caduceia** França

*Caduceia* França, 1918, Bull. Soc. Port. Sci. Nat., 8:94 (type species, *C. theobromae* França).—Kirby, 1938, Univ. Calif. Publ. Zoöl., 43:2.

*Diagnosis.*—Size large, in known species average length 62–88μ, range 35–138μ, average width 26–58μ, range 18–75 (89)μ;[1] three long, slender anterior flagella; trailing flagellum slender, usually shorter than the body; cresta usually relatively short, length 1–12μ; parabasal body coiled around axostyle loosely or tightly in 2–20 turns, usually simple but sometimes with short or long outgrowths that spiral with the rest; capitulum of axostyle moderately developed, chromatic shield usually present; trunk of axostyle tapered to a filamentous end enclosed within the cytoplasm, as in *Devescovina;* nucleus large, longer diameter usually longitudinal, abundance of deep-staining material present, and formation of clear space under membrane, as is typical of *Devescovina,* may occur; body covered with a dense investment of short spirochaetes; short *Fusiformis*-like rods adherent to restricted areas or generally distributed on some species, absent from others.

#### TAXONOMY AND DISTRIBUTION

França (1918) recognized no relationship between *Caduceia* and *Devescovina,* since he supposed the former to be covered with cilia. In his opinion, the parabasal body, axostyle, and nucleus admitted comparison with those structures in *Lophomonas* and *Joenia,* and the ciliation of the body resembled that of *Spirotrichonympha* (*Leidya*); consequently, he regarded *Caduceia* as a hypermastigote transitional between the Lophomonadidae and the Holomastigidae.

Recognition by protozoölogists of the real nature of the adherent spirochaetes on flagellates in termites led to a reduction of *Caduceia* to synonymy with *Devescovina.* This was a logical conclusion, especially in the absence of any exact definition of the characteristics of *Devescovina,* since *Caduceia* is indeed very close to *Devescovina.* Separation from that genus, in fact, is subject to differences of opinion.

Grassé (1937*a*), having abandoned the earlier views on synonymy expressed by Duboscq and himself (1927), recognized the genus *Caduceia* for *C. theobromae.* He stated that the genus merits autonomy because of the small dimensions of the trailing flagellum, the absence of the costule, and the size of the parabasal apparatus. The costule, termed a cresta in this paper, is present in *Caduceia* as in all Devescovininae. The other two points are well taken, however, and to them the large size of the body might be added. These, of course, are but differences in degree of development of certain structures of *Devescovina;* there are no different structures, and in type of nucleus and axostyle the two are identical. The two genera are therefore not sharply separated. If we should find a *Caduceia*-like form with a large trailing flagellum, or a small parabasal apparatus, there might be need of taxonomic revision to place it.

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[1] All measurements are of material fixed in Schaudinn's, Flemming's, or Hollande's fluid.

*Caduceia* is not a common genus, only nine species of Kalotermitidae having been found infected. Four of the six species are restricted to one host each. The species which I saw all occur in termites of Africa, Java, and Ceylon. *C. pruvoti* extends the range to the Loyalty Islands near Australia; but, as I have not studied it, its assignment to *Caduceia* is based only on the published description. No representative of the genus has been found in the many Australian and American termites examined. It is noteworthy also that the two African species are closely related to one another, and so also are the two from Java.

## GENERAL MORPHOLOGY

The foregoing diagnosis is slightly revised from that formerly published by me (1936), owing to more complete studies.

The average lengths of several species of *Devescovina* approach or equal the lower averages in *Caduceia,* but in most such instances the width is very much less. The largest species of *Devescovina, D. vittata,* equals the smallest species of *Caduceia, C. bugnioni,* in length and width. It is, however, clearly a *Devescovina* in its broad, long trailing flagellum and its rather small parabasal body; and it resembles other species of the genus in the adherent *Fusiformis*-like rods.

Among the species of *Caduceia* there is a good deal of uniformity in the anterior granules. The blepharoplast group, to which most of the organelles connect, sometimes appears as a number of separate granules in a compact aggregation. In some material of *C. monile* (pl. 14, figs. 19, 20) the blepharoplast is large, and consists of small granules imbedded in a stainable matrix; in other preparations the matrix cannot be seen. Near this blepharoplast is usually a second granule, which is relatively very large in *C. monile.* It is at the end of one of the two roots of the three anterior flagella, and is connected by a fine filament to the blepharoplast. The other flagellar root passes directly to the blepharoplast. In *Devescovina,* structures comparable to these occur only in *D. tendicula,* and to a lesser extent in *D. insolita.* The degree of development is small, however, and in other respects the differences of those species from *Caduceia* are marked.

The trailing flagellum is a relatively slender cord, shorter than the body in the species which I have studied. In *Caduceia pruvoti* it is represented by Duboscq and Grassé (1929) as not surpassing the body in length. In *Devescovina* the trailing flagellum is typically much longer than the body, although usually not equal to twice that length, and it is often stout or bandlike. The three anterior flagella of *Caduceia* are also typically shorter than the body. The body in *Caduceia* has increased in size more than the flagella.

Like the flagella, the cresta has undergone little development in the genus; in some species, indeed, it is relatively minute in size. The crestas of *Caduceia*

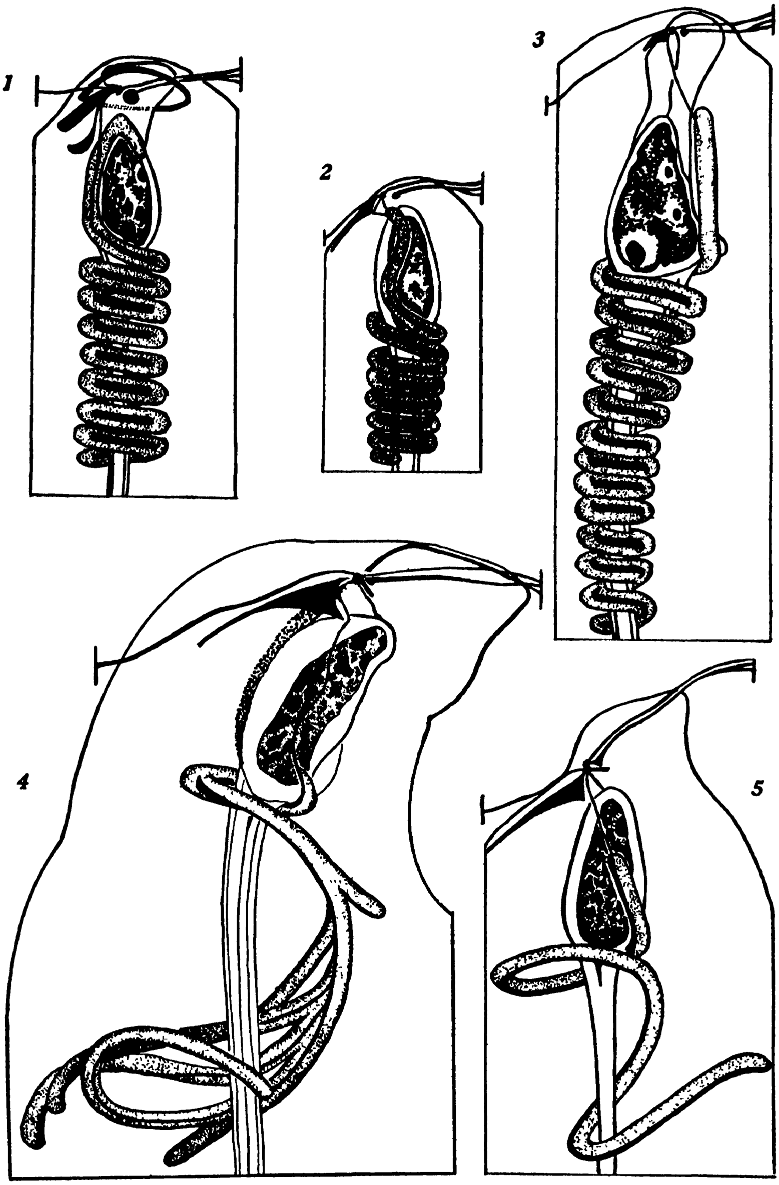

Fig. A. Diagrams of mastigont structures of species of *Caduceia*. All figures show the blepharoplast; roots of the anterior flagella, one of which terminates in an enlargement; cresta; nucleus; anterior part of trunk of axostyle; parabasal body and parabasal filament. × 2330. 1. *Caduceia monile* sp. nov. from *Neotermes tectonae*, showing also the clavate crestal accessory, the ring, and outline of the capitulum. Notable is the blade form of the cresta. 2. *C. bugnioni* sp. nov. from *Neotermes greeni*. 3. *C. kalshoveni* sp. nov. from *Neotermes dalbergiae*, showing also the outline of the capitulum and the nuclear rhizoplast. 4. *C. nova* (Grassi), showing also the nuclear rhizoplast and the granular chromatic shield. 5. *C. theobromae* França from *Kalotermes jeannelanus*, showing also the rod that extends from the blepharoplast.

*theobromae* (fig. A, 5), *C. nova* (fig. A, 4), and probably *C. pruvoti* (fig. C) resemble that of *Devescovina lemniscata* in size and shape, but because of the much greater size of the organisms they are relatively small. The cresta of *C. kalshoveni* (fig. A, 3) is as small as in almost any devescovinid flagellate, and those of *C. monile* (fig. A, 1) and *C. bugnioni* (fig. A, 2) are but little larger.

In the anterior region of the body there are some unusual structures in certain species of *Caduceia.* Among these are the rings at the base of the papilla in *C. monile* and *C. kalshoveni* (pl. 14, fig. 19; pl. 13, fig. 16). A short rod like that attached to the blepharoplast in *C. theobromae* (fig. A, 5) and *C. nova* (pl. 11, fig. 5) occurs also in *Devescovina insolita. C. monile* has a unique structure in the clavate crestal accessory (pl. 14, fig. 19). A crestal accessory occurs also in some other devescovinids, and the paracrestal filament of *Macrotrichomonas pulchra* may be an equivalent structure.

The advanced development of the parabasal body is a feature of the genus. It is spiraled around the axostyle, as in *Devescovina* and *Metadevescovina,* and usually it has many close turns. *Caduceia theobromae* and *C. nova,* with their loosely wound parabasals, stand apart from the other species. Outgrowth of branches or rami is particularly characteristic of *C. nova* (fig. A, 4), but occurs also in some specimens of *C. theobromae. C. nova* is the most advanced example of this outgrowth in species of Devescovininae in which the principal element of the apparatus is spiraled around the axostyle. Rami, which are similarly spiraled, grow out at intervals along this element; and they usually increase in length sufficiently to reach about the same level posteriorly.

The chromophile element of the parabasal apparatus (pl. 14, fig. 20) is often very conspicuous. At the inner edge of the spiral it is a thread, or is broadened to a band. It sometimes appears broader in certain Flemming-fixed than in Schaudinn-fixed material. The other substance may end near the anterior end of the nucleus, or farther posteriorly; only in *Caduceia monile* does it curve around the anterior end of the nucleus in a hook (pl. 14, fig. 21). When it ends near the posterior part of the nucleus (*C. theobromae, C. nova*), the parabasal filament continues alone to the blepharoplast. When it extends farther anteriorly, the parabasal filament separates from it at a distance from the anterior end, running close to the anteromedial edge of the cresta to the blepharoplast (*C. bugnioni, C. monile*), or continues with it as far as it goes (*C. kalshoveni*). In Delafield-stained preparations the parabasal body does not show the heterogeneity that is evident in some species of *Metadevescovina.*

The chromatic shield, which occurs also in some species of *Devescovina,* is well developed in all species of *Caduceia* that have been studied except *C. kalshoveni,* in which it seems definitely to be absent. It is a rather narrow cresta-shaped group of granules in most species, but in *C. bugnioni* it covers all of one side of the nucleus (pl. 11, fig. 10). In *C. monile* it extends only halfway or less along the nucleus or the moderately developed capitulum (pl. 14, fig. 22).

The trunk of the axostyle is like that of *Devescovina.* It tapers to a filament posteriorly (pl. 11, fig. 6) and is entirely enclosed in the cytoplasm. In preserved material its posterior part often is curved forward within the cytoplasm (pl. 10, fig. 2). This type of curvature occurs also in some species of *Devescovina,* but has not been observed in the *Foaina-Metadevescovina* type of axostyle, with its projecting cusp.

In the shape, structure, and position of the nucleus (fig. A) *Caduceia* is closely related to *Devescovina.* There is no irregularity of outline like that characterizing nuclei of certain species of *Foaina* and *Metadevescovina.* The longer diameter is usually in the longitudinal axis of the body, with the blepharoplast granules near the anterior continuation of this same axis. The contents of the nucleus are coarsely granular and deep-staining, and a space under the membrane is usually present in Schaudinn-fixed material. In the following account of *C. nova* it is stated that the breadth of this space may vary with different fixatives, but occurrence of the space nevertheless indicates a difference from nuclei of the other main devescovinid type. *C. bugnioni* and *C. theobromae* show well the two types of pointed posterior prolongation. In the former species it is always simply a continuation of the chromatin mass (pl. 11, fig. 10); in the latter it is always separate from this, and seems to be appended to the nuclear membrane (pl. 10, fig. 1).

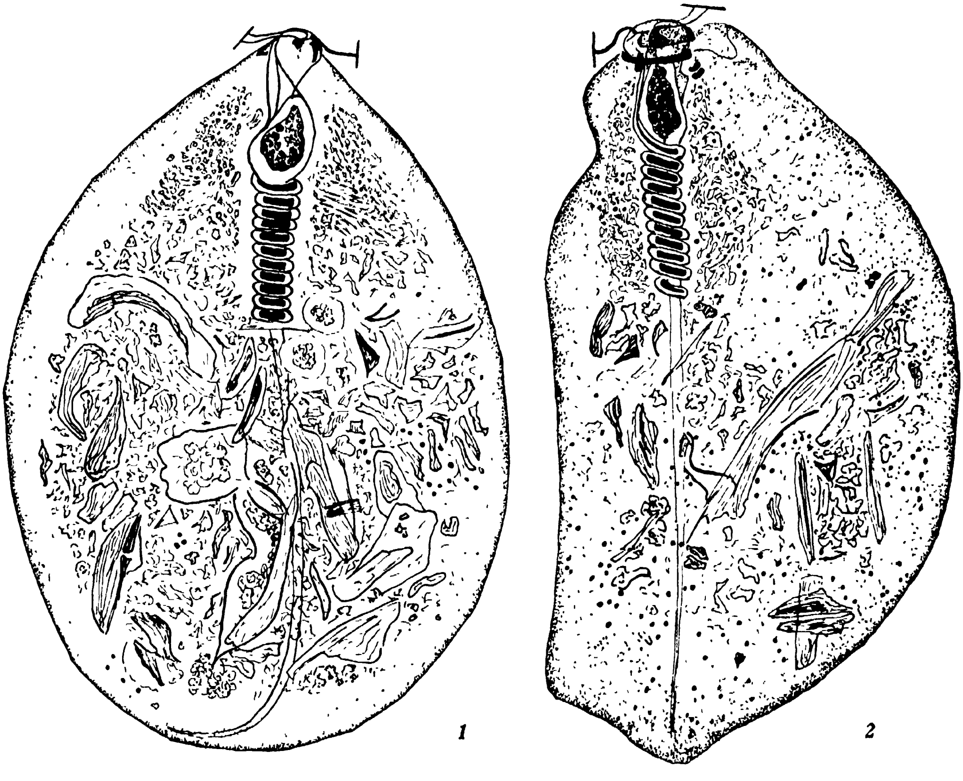

Fig. B. 1. *Caduceia kalshoveni* sp. nov. from *Neotermes dalbergiae.* 2. *C. monile* from *Neotermes tectonae.* Distribution of particles of wood in cytoplasm. There is a general distribution of small and moderate-sized particles in the cytosome posterior to the parabasal body. In the cytoplasm around the parabasal body and nucleus are numerous, closely packed, minute particles of wood. x 1150.

In *Caduceia monile* and *C. kalshoveni* there is a peculiarity in the distribution of wood (fig. B) similar to that previously reported in *Devescovina tendicula* and *D. vittata* (pp. 38, 54, fig. D, 4, 5, first part of this monograph). Small particles of wood are densely packed in the region of the cytoplasm surrounding the nucleus and parabasal body. The particles are elongated in form, and are remarkably uniform in size and shape. Wood particles that are often of different size and shape from these are present elsewhere; but the aggregation is striking and occurs in all specimens of the two species.

A dense investment of short adherent spirochaetes, which seem to be of the same type in all species, is universal. The microörganisms are usually much shorter than those on any species of *Devescovina*. Longer adherent spirochaetes are fewer in number and less constant in occurrence.

The adherent *Fusiformis*-like organisms that occur on three of the species are much shorter than those characteristic of *Devescovina*, and are more slender than the short ones on *D. elongata*. Their distribution is unusual in that they are confined to a restricted, very sharply bounded area in *Caduceia theobromae* and *C. nova;* and in *C. bugnioni*, where the distribution is more general, they tend to be arranged in transverse bands (pl. 11, fig. 7).

### KEY TO SPECIES OF CADUCEIA

1. Parabasal body spiraled in a few broad, loose turns .................... 2
   Parabasal body spiraled in many close turns .................... 3
2. Parabasal body unbranched in most specimens; rami, if present, usually short .................... *C. theobromae*
   Parabasal body generally with several rami .................... *C. nova*
3. Cresta length less than 5$\mu$ .................... 4
   Cresta length more than 6$\mu$ .................... *C. pruvoti*
4. Short rodlike bacteria adherent to most of the surface, often in transverse bands; anterior ring absent .................... *C. bugnioni*
   No adherent rods; anterior ring present .................... 5
5. Ring stout, 7–10$\mu$ in diameter in average-sized specimens; cresta bladeformed; parabasal body with hook-shaped anterior part .................... *C. monile*
   Ring more slender, broader; cresta smaller, subtriangular; parabasal body ending without enlargement near the anterior end of nucleus, no parabasal hook .................... *C. kalshoveni*

### MORPHOLOGY AND DIAGNOSIS OF SPECIES OF CADUCEIA

#### **Caduceia theobromae** França

(Pl. 10, fig. 1; fig. A, 5)

*Caduceia theobromae* França, 1918, Bull. Soc. Port. Sci. Nat., 8:94, pl. 2, figs. 1–8, figs. A, B, C-3, D-2.—Grassé, 1937, C.r. XIIe Congr. Int. Zool., 1324, pl. 57, figs. 1–3.—Grassé, 1937, C.r. Soc. Biol., 125:918.—Kirby, 1938, Univ. Calif. Publ. Zoöl., 43:3, pl. 1, figs. 1–7; pl. 2, fig. 8; pl. 6, figs. 42–44; figs. A, B.—Grassé, 1938, Bull. Soc. Zool. France, 63:114, figs. 2, 3.

*Devescovina* (*Caduceia*) *theobromae* França. Duboscq and Grassé, 1927, Arch. Zool. exp. gén., 66:452.

*Devescovina theobromae*. Bernstein, 1928, Arch. Protistenk., 61:30.

*Type host.—Neotermes gestri* Silvestri. Island of St. Thomas. (França.)

***Additional hosts***

*Neotermes aburiensis* Sjöstedt. Ivory Coast. (Grassé.) Near Bingerville.
*Kalotermes jeannelanus* Sjöstedt. East Africa.
T-2013. Mount Meru, T.T. (Slides TP-1083:6, 8.)
T-1063–1065. Moshi, Tanganyika Territory.
T-1092–1094. Taveta Forest, Kenya.
T-3015. Near Rutshuru, Belgian Congo.
*Kalotermes* (s.l.) sp. nov. Transvaal, South Africa.
T-4240. Near Nylstroom. (Slides TP-3069:12; 3073:7.)
T-4252. Near Duivels Kloof. (Slide TP-3072:10.)

***Diagnosis.***—(From *Kalotermes jeannelanus*): length 69 (57–112)μ; width 33 (21–51)μ; trailing flagellum a slender cord, usually shorter than body; cresta length 5–8μ; parabasal body generally spiraled in broad, loose, uneven coils, number of turns 2–5, averaging 3; chromatic shield of small, deep-staining granules present; nucleus 9–13 by 4.5–7μ; slender rod-shaped microörganisms adherent to a restricted area at the posterior end; slender spirochaetes, often 6–8μ long, forming a dense coat over the rest of the surface; longer spirochaetes often adherent at the place where the other two types of microörganisms meet. (From *Kalotermes* sp. nov. T-4240): length 70 (49–93)μ; breadth 41 (25–56)μ; cresta length 6.8 (5.1–8.5)μ; nucleus 13 (10–14) by 6 (5–7)μ.

My account of this flagellate (1938*a*) was published before Grassé's description (1937*a*) was available in Berkeley, either in the Proceedings of the Congress or as a separate. Because no citation had appeared, I was ignorant of the work although it had been delivered to the Congress in 1935. Grassé's studies had already revealed correctly the devescovinid organization of the flagellate.

Grassé gave the name of the type host as *Neotermes gestroi.* The specific name is spelled *gestri* in Silvestri's original description, however, although it probably should have been formed as *gestroi.* According to its author (Sjöstedt, 1925), *Neotermes aburiensis,* which was the source of Grassé's material, is closely related to *N. gestri.*

The measurements reported by me (1938*a*) are incorrect, owing to use of a wrong calibration. Revised measurements, which are considerably less for body size, cresta, and nucleus, are given in the diagnosis. Grassé reported an average length of 100μ, indicating a much greater length for the specimens in *Neotermes aburiensis;* but the breadth, 30–35μ, is near the average of my material from East and South Africa. The trailing flagellum as first described by Grassé (1937*a*) was shorter than that seen in my specimens, but his later figures (1938) agree with my observations.

According to Grassé, each flagellum originates in a separate granule, the three granules of the anterior flagella being so close together as to appear as one. The parabasal is said to originate from still another granule. I described two main granules, one at the end of one of the two flagellar roots, the other the blepharoplast group to which this granule and various organelles, including the nuclear rhizoplast and a short rod, are connected. Further observations have verified that account (fig. A, 5). The flagellar granule is probably the one which Grassé considered to be the group of three blepharoplasts of the anterior flagella, and possibly it is compound. The blepharoplast group is composed of several granules. It may well be true that each separate structure joins a different granule in this group, but it is impossible to ascertain that fact. Grassé did not describe the nuclear rhizoplast and the short rods.

The cresta is a conspicuous structure in suitably prepared material, but Grassé (1937*a*) did not figure it, and he mentioned it only in the statement that he was not sure there is not a fibril homologous with the costule of *Devescovina.* Later in the same paper he stated that *Caduceia* lacks a costule. In 1938, however, he figured a structure that is unmistakably the cresta, but made no comment on it in the text.

The structure which I described as the chromatic shield had also been observed and figured by Grassé, who regarded it as an axostylar lamella. Is it actually a part of the capitulum of the axostyle? Grassé compared it to the anterior extension of the axostyle shown along one side of the nucleus in *Eutrichomastix colubrorum* (Grassé, 1926, p. 511), and also to the anterior prolongation in *"Devescovina" hilli.* Duboscq and Grassé (1927) had called this latter structure the suspensory lamella of Janicki. These comparisons appear to me invalid. The chromatic shield is a group of granules which do lie against a part of the capitulum, but it is not the capitulum itself.

Grassé described the parabasal body accurately, with respect to the beginning of the main substance along the posterior part of the nuclear membrane, and the filament connecting this to the blepharoplast. He seems to have regarded this filament as separate from the chromophile border he described along the full length of the flattened structure. The continuity of the parabasal filament from the blepharoplast to the posterior end is, however, unmistakable.

The main substance of the parabasal body begins in a somewhat variable position in relation to the nucleus, often near the middle (fig. A, 5) or in the posterior part. In some specimens, however, especially daughter individuals of recent division, it continues to the blepharoplast, as it does in instances of nuclear division.

Grassé gave a new interpretation of the row of granules França showed paralleling the parabasal. Repudiating the earlier suggestion of Duboscq and Grassé (1933) that they were vesicles about to detach, he concluded that they were chromophile substance altered by the fixative. I similarly believed that they might represent the parabasal thread. However, it is doubtful that the filament is broken up into granules of such regularity by Schaudinn's fluid, which Grassé stated to be the reason França interpreted it as he did. I have seen the parabasal filament separated in part into fragments, however. Cytoplasmic granules often adhere along the parabasal body, and it may be that França observed these but exaggerated their regularity.

In the preparations from *Kalotermes* sp. of the Transvaal a larger proportion of *Caduceia theobromae* with branched parabasals was found than in the East African material (pl. 10, fig. 1). In most instances of branching, the rami, one to several in number, are very short. Long rami reaching posteriorly as far as the end of the main stem of the parabasal, the existence of which is characteristic of *C. nova,* occur very infrequently. When such long rami do occur, there is seldom more than one.

Grassé stated that two or even three parabasals occur rarely, usually in only one or two specimens in a smear. He considered it likely that the supplementary structures grow out from the original one, but he nevertheless recognized a possibility of longitudinal cleavage. I do not agree with him, however, in his use of the phrase "two or three parabasal bodies" for the situation in which there are rami; actually, as is shown in his figure 3, there is a single parabasal apparatus.

Grassé (1937*a*, 1938) gave an exhaustive account of the microörganisms adherent to the surface. I, too, reported the same types: short spirochaetes, often 4–6μ long, covering almost the entire surface; rods adherent to a restricted area at the posterior end; and an occasional group of longer spirochaetes at the posterior end. Grassé noted that the longer spirochaetes often adhere at the region where the small spirochaetes and the rods meet.

Grassé made no mention of the slender rods that usually occur in abundance in the cytoplasm of *Caduceia theobromae*, as in that of *C. nova* (Kirby, 1936). He stated, however, that *Fusiformis* (the rods adherent externally) sometimes penetrate into the interior, but are not very abundant except in the so-called subcystic *Caduceia*, where they multiply actively. These "subcystic" *Caduceia* occur, he stated, in termites before and after the imaginal molt, from which stage I have no material. The normal abundance of the cytoplasmic rods was not, therefore, recognized by him; and it is not certain whether he identified the internal rods of the type which I described with the externally adherent rods. They do not have the same appearance, but of course they might be the same thing under different conditions. That is, however, at least no more likely than that they are two different microörganisms, as seems to me probable.

Grassé (1938) reported the rather frequent formation in *Caduceia theobromae* of pockets lined with spirochaetes, like those which I described (1936) in *Pseudodevescovina uniflagellata;* and he further noted the closing of these to form intracytoplasmic vacuoles, which contain spirochaetes. I have occasionally seen these pockets in prepared material of *C. theobromae*, but they are not frequently formed.

### **Caduceia nova** (Grassi) Kirby

(Pl. 10, figs. 2–4; pl. 11, fig. 5; fig. A, 4)

*De Vescovina nova* Grassi, 1917, Mem. R. Accad. Lincei (5) 12:380, pl. 9, figs. 28–32.

*Caduceia nova* (Grassi). Kirby, 1936, Quart. Jour. Micr. Sci., 79:326, pl. 16, figs. 32–37.

*Type host.*—*Neotermes erythraeus* Silvestri. Eritrea.

T-312. (Silvestri.) (Xenosyntype slides TP-321:1, 2.)

*Additional host*

*Neotermes* sp. Tanganyika Territory.

T-2012. Mount Meru, near Usa. (Homosyntype slides TP-1082:9, 13, 26.)

*Diagnosis.*—(From type host): length 88 (64–114, occasionally 138)μ; width 47 (32–67, occasionally 76)μ; trailing flagellum a slender cord, shorter than the body; cresta length 9–12μ; parabasal body with proximal element turned in a variable, usually wide loop around the axostyle just posterior to the nucleus, then in a long, loose spiral often of about 2 turns, with 1–6 long rami, of caliber equal to the first part, attached at various points posterior to the first loop and turned parallel to it and one another; chromatic shield present; capitulum of axostyle moderately developed; trunk of axostyle tapered to a filamentous end completely enclosed in the cytoplasm; nucleus with broad space between membrane and chromatin mass, 15 (12–17) by 7.5 (6–9)μ; body invested with a coat of spirochaetes 4–6μ long; short,

**slender rods adherent to a restricted area, circular in outline, at or near the posterior end, which lacks the short spirochaetes. (From *Neotermes* T-2012): length 72 (51–93, occasionally 116)μ; width 33 (26–46)μ; cresta length 8–10μ; main stem of parabasal body as in type, with 0–8 rami, 3–6 in most specimens; nucleus 11 (10–12) by 5.3 (4.5–7)μ.**

The material available for study at the time of my earlier account (1936) of this species was very limited. Discovery of the species in the more numerous preparations from the termite of Tanganyika Territory renders possible a more complete and accurate description. Furthermore, comparative studies made since that paper went to press have aided in the interpretation of certain structures.

The granules at the base of the flagella and other structures, although described with a fair degree of accuracy, were not altogether correctly interpreted. The blepharoplast group is more or less compact and apparently consists of four granules. From this group arise the following structures (pl. 11, fig. 5): a rhizoplast, which meets the nuclear membrane; the cresta, which is attached by a short, slender fibril; the trailing flagellum; the parabasal filament, the proximal part of which passes close to the anteromedial edge of the cresta; a short, deep-staining rod, which extends free into the cytoplasm, exactly like that in *Caduceia theobromae;* and the two roots of the three anterior flagella. In *C. theobromae* one of these roots terminates at a relatively large granule connected by a filament to the blepharoplast group. A similar granule is usually present in *C. nova* from *Neotermes erythraeus;* often it is as large as the blepharoplast group. In the specimens from *Neotermes* T-2012, however, this flagellar granule is not so distinct; the somewhat enlarged end of the root is connected directly to the blepharoplast group.

*Caduceia nova* resembles *C. theobromae* closely in every characteristic except the parabasal apparatus. This, too, is the same in corresponding parts in the two species, but that of *C. nova* almost always has long rami, whereas that of *C. theobromae* seldom does, and there are more rami in *C. nova.*

In my earlier figures the anterior part of the parabasal body was drawn stout where it extends along the nuclear membrane, although, as noted in the text, only the thread could be seen clearly. Inclusion of the other substance in this anterior part is not representative of the usual condition. Exactly as in *Caduceia theobromae,* the main substance of the parabasal usually ends against the middle or posterior part of the nucleus, and the parabasal thread continues alone to the blepharoplast (fig. A, 4).

The first transverse loop has the same shape in the two species. The rami, which develop by budding, occur along the main stem of the parabasal posterior to this loop (pl. 10, figs. 2–4). In *Caduceia nova* from *Neotermes* T-2012 the number of rami in 57 specimens was as follows: 0 in two specimens, 1 in three, 2 in two, 3 in ten, 4 in twelve, 5 in fifteen, 6 in nine, 7 in three, 8 in one. A short secondary branch of one of the rami was once observed (pl. 10, fig. 3).

The nucleus is ellipsoidal, rounded at both ends, and elongated, with the longer diameter longitudinal and in line with the trunk of the axostyle (pl. 10, fig. 69). The membrane is distinct and the chromatin mass consists of numerous, irregular, deep-staining granules. The nucleolus is relatively large, and is situated opposite a depression in the chromatin mass. Between the membrane and the mass is a space. As was noted in the earlier description, this may be very broad. It was broader in Schaudinn-fixed preparations than when Flemming's fixative was used; this material, in fact, shows clearly the result of shrinkage in the former reagent. Some space was always present, however, and in some Flemming material it is broad, whereas in the same preparations no space appears in the nucleus of *Pseudodevescovina ramosa.*

Posterior to the nucleus is a conical structure extending into or along the trunk of the axostyle (pl. 10, fig. 4). It is not connected to the chromatin of the nucleus, and it appears to be applied to the nuclear membrane rather than to be a prolongation of the nucleus. The conical structure is present at the posterior end of parasitized nuclei in which all chromatin has been destroyed.

The adherent microörganisms are similar to those on *Caduceia theobromae.* Spirochaetes, often 4–6$\mu$ long, adhere to all the body surface not occupied by the rods (pl. 10, fig. 2). The investment is as dense as in *C. theobromae* and *Pseudodevescovina uniflagellata,* as has been ascertained by the study of more adequately stained material than was available at the time of publication of my earlier description. The rods, which are often 2–5$\mu$ long and occur in parallel arrangement in groups, adhere to a sharply circumscribed area at the posterior end (Kirby, 1936). The boundaries of this area are sharper than was indicated in the figure published previously, and the diameter of the area is more variable than was stated in the text. There are also longer spirochaetes adherent near the posterior end.

Pockets containing spirochaetes have been observed in a few specimens, as in *Caduceia theobromae* (p. 101).

### **Caduceia bugnioni** sp. nov.

(Pl. 11, figs. 6–10; pl. 12, figs. 11–13; fig. A, 2)

"Trichonymphides du *Calotermes greeni* Desn.," *partim,* Bugnion and Popoff, 1910, Mém. Soc. Zool. France, 23:133, pl. 5 (in part).–De Mello, 1921, Arqu. Ind.-Port. Med. Hist. Nat., 1:164, pl. 2 (in part).

*Type host.—Neotermes greeni* Desneux. Ceylon.

T-310. (Cleveland-Collier.) (Syntype slides TP-253:124, 75, 133.)

*Diagnosis.*—Length 62 (48–80)$\mu$; width 26 (18–40)$\mu$; three anterior flagella about 30–35$\mu$ long; trailing flagellum slender, shorter than body; cresta length 2.5–4$\mu$, averaging 3$\mu$; parabasal body coiled closely around trunk of axostyle 3½–7 times, usually 5 or 6, diameter of coil decreasing gradually posteriorly, successive turns very close together; dense group of granules in or on the capitulum on the right side of the nucleus, forming chromatic shield; nucleus 7.6 (6.3–9.2) by 3 (2.3–4)$\mu$, chromatin mass pointed posteriorly; rod-shaped bacteria 1½–3$\mu$ long adherent to body surface, arranged in a generally longitudinal direction, often grouped in tranverse bands; slender spirochaetes 4–6$\mu$ long forming a dense coat over entire surface.

In addition to *Caduceia bugnioni, Neotermes greeni* contains two species of *Foaina* and a species of *Stephanonympha.* In the figures by Bugnion and Popoff flagellates of the three genera are represented. Their first type, in which they observed "une sorte d'entonnoir entouré de bourrelets brilliants à direction transverse," and figured the parabasal body, which is referred to in that quotation, is *C. bugnioni.* The upper right figure probably represents

*Stephanonympha*, but it is not certain what their second form with invaginated "oral extremity" is. They mistook *Foaina* for young forms of the other flagellates. They observed the inclusion of wood fragments within the Protozoa, and expressed their belief that the flagellates contribute to the nutrition of the termite by digesting wood, multiplying each day in great numbers, dying, and being digested in their turn. They stated that if termites were starved for twenty-four hours the "ciliated balls" (*Stephanonympha* and *Caduceia*) were found immobile.

De Mello (1921) reproduced Bugnion and Popoff's description and figures of the flagellates from *Neotermes greeni*, but he was unable to suggest an identification of the forms.

The measurements reported in the diagnosis were made from a hundred specimens. The flagellates are very abundant in their hosts. A few were found on some smears of *Cryptotermes dudleyi* from Ceylon, but this undoubtedly was in consequence of contamination of the preparations with material from *Neotermes greeni*.

The blepharoplast group (pl. 11, fig. 9) consists of several closely aggregated granules. Generally the granules are not separately distinguishable, but sometimes there appear to be at least two or three. The anterior flagella arise as two roots, one of which is the stouter. The slender root runs directly, without enlargement, to the blepharoplast group. The stouter one ends at a large, deep-staining granule, which is connected by a delicate fibril to the blepharoplast. The root meeting this granule apparently is the one that divides into two flagella. This granule stains with iron-haematoxylin more deeply than do the other granules, and is visible when they are not. It stains with Delafield's haematoxylin when the others do not. The trailing flagellum is cordlike and becomes very slender in its distal portion (pl. 11, fig. 6). It is somewhat stouter than the anterior flagella, but its length is less than that of the body. The cresta is a narrow, subtriangular structure about 3$\mu$ long, varying from about 2.5 to 4$\mu$ (pl. 11, fig. 6). It has been observed projecting beyond the edge of the body, usually if not always covered by cytoplasm (pl. 11, fig. 10). The nuclear rhizoplast is a short, slender filament extending from the blepharoplast group to the nuclear membrane (pl. 11, fig. 9).

The parabasal body is coiled tightly around the trunk of the axostyle just posterior to the nucleus, and the first turn often surrounds the posterior end of the nucleus itself. The longitudinal anterior part is about as broad as the rest, but is flattened. It extends along the nuclear membrane to the anterior end of the nucleus, not reaching to the blepharoplast (pl. 11, fig. 8; fig. A, 2); and its anterior end is often somewhat enlarged (pl. 12, fig. 11).

The chromophile element in the first turn of the spiral is almost as broad as the parabasal body (pl. 11, fig. 9). Posteriorly it diminishes in size, and anteriorly it is reduced more sharply to a filament. Along the longitudinal part it runs parallel to the Delafield-staining substance (pl. 11, fig. 9), but is separated from it in its anterior portion, where it curves outward to come close to the cresta, then turns at a sharp angle to pass to the blepharoplast group (pl. 11, figs. 8, 9).

The chromatic shield is a group of small, uniform, regularly distributed granules against the left side of the nucleus (pl. 11, figs. 6, 10). These granules evidently are on or in the capitulum. The group is of constant occurrence and form. The capitulum extends anterior to the nucleus and into the papilla. Its outlines are somewhat irregular, and are sharply defined in heavily stained iron-haematoxylin preparations (pl. 11, fig. 9; pl. 12, fig. 13).

The trunk of the axostyle decreases in diameter to the posterior end, where it is very slender and pointed (pl. 11, figs. 6, 7). In many specimens its end does not reach to the end of the cytosome. In others it is longer than the cytosome proper, and either extends into a pointed cytoplasmic process or is curved so as to remain enclosed in the body. In many specimens the trunk stains deeply with iron-haematoxylin. When the axostyle is suitably destained, a fibril appears in its center (pl. 11, fig. 6).

The chromatin mass in the nucleus is composed of small and large deep-staining granules, and there is a peripheral nucleolus. The chromatin mass is pointed posteriorly and often also anteriorly (pl. 12, fig. 13); and in most fixed material a clear space separates it from the membrane.

In the cytoplasm the conspicuous inclusions are granules and fragments of wood. Among the granules are some of moderate or large size which are sometimes very abundant, and these often are aggregated into groups. They are probably endozoic microörganisms, and, with other endozoic forms in this flagellate, will be considered later. Wood fragments are sometimes observed to be surrounded by close-fitting vacuoles. In one specimen these vacuoles were covered with a layer of closely and uniformly distributed granules (pl. 12, fig. 12).

Invariably present are two types of microörganisms adherent over the whole body surface of *Caduceia bugnioni.* The more conspicuous of these are slender spirochaetes, about 4 to 6$\mu$ long, forming a dense cilialike investment (pl. 11, figs. 6, 7). They cover even the papilla. The other microörganism is a short, slender rod, adherent, as in *Devescovina,* by its full length in a generally longitudinal direction. The rods vary in length from about 1½ to 3$\mu$. They tend to be rather regularly arranged in transverse bands around the body, with narrow clear spaces between adjacent bands (pl. 11, fig. 7). They are not present on the papilla.

### **Caduceia monile** sp. nov.

(Pl. 13, fig. 18; pl. 14, figs. 19–23; fig. A, 1; fig. B, 2)

*Type host.*—*Neotermes tectonae* Dammerman. Java. Sumatra.

T-311. Djember, Eastern Java. (Cleveland-Collier.) (Syntype slides TP-251:7, 16.)

T-4528, 4529. Kateman, Sumatra. (Homosyntype slides TP-3244:3; 3245:3.)

T-4542. Telawa, Java. (Homosyntype slides TP-3227:19, 3.)

*Diagnosis.*—Length 75 (46–110, exceptionally 131)$\mu$; width 43 (27–64)$\mu$; rounded stopper-formed protuberance in which the anterior structures are situated often present at anterior end; stout ring, diameter 7–10$\mu$ in average-sized specimens, at base of this protuberance; trailing flagellum a slender cord, about half the length of the body; cresta blade-formed, not narrowed in distal portion, length about 3$\mu$; club-shaped accessory structure close to cresta; parabasal body coiled tightly 5–15 turns, generally 9–12, hook-formed around the anterior part of the nucleus; granular chromatic shield present on anterior part

**of crestal side of nucleus; nucleus 10 (9–11) by 6.4 (5.4–7.4)$\mu$; entire surface invested with short spirochaetes, like those on *Caduceia bugnioni; Fusiformis*-like rods absent.**

The body is very stout in build. At the middle of the anterior end there projects a rounded protuberance commonly overhung anteriorly, like a portion of the lip of a stopper, on the side where the anterior flagella become free. This protuberance rises sharply from a broad base, and in it are all stuctures anterior to the nucleus (pl. 13, fig. 18; pl. 14, figs. 19, 22).

Immediately beneath the surface of the body at the base of the protuberance is a ring that stains deeply with iron-haematoxylin (pl. 14, fig. 19). Its thickness, although somewhat variable, is often about equal to that of the chromophile element of the parabasal apparatus. Its suggestion of a necklace or collar is the source of the specific name. In a number of specimens that show no evidence of being in division or postdivision phases the ring is open in one place. It seems to be without connection with other organelles.

In the anterior part of the protuberance are two large granules (pl. 14, figs. 19, 20). One of these stains more deeply than the other, and shows in much destained material when the other is invisible. Its outline is somewhat irregular; often it appears quadrangular in optical section. The stouter posterior root of the anterior flagella, which divides into two flagella, connects directly with this granule. Probably a fine filament connects this granule to the second one.

The second granule, which is situated close to the other at the same transverse level, is the blepharoplast to which most of the organelles are connected. Often it is somewhat smaller than the other granule. In suitably differentiated material it is shown to be actually a group of small granules, which probably are imbedded in a matrix of less intense-staining substance (pl. 14, figs. 19, 20). It resembles Janicki's figure of the blepharoplast of *Devescovina hawaiensis* more clearly, in fact, than does that structure in the flagellate he studied.

From the blepharoplast there passes ventrally along the anterior edge of the papilla the slender root of the third anterior flagellum, which is, in contrast to the posterior root, no stouter than the free part of the flagellum. From the other side of the blepharoplast emerges the small trailing flagellum (pl. 13, fig. 18), which is a slender cord scarcely more than half the length of the body. The well-defined nuclear rhizoplast (pl. 14, fig. 19) has the characteristic bend observed in various species of *Macrotrichomonas*. It passes from the posterior end of the blepharoplast obliquely to a position behind the flagellar granule, then bends and extends posteriad to meet the anterior nuclear membrane. The rhizoplast is stouter in its posterior portion than in its anterior portion.

The cresta, which is attached to the blepharoplast near the point of attachment of the trailing flagellum, is shaped like a paring-knife blade instead of being narrower distally, as in most devescovinids (pl. 14, figs. 19, 20; fig. A, 1). It has a breadth of about 1$\mu$. Close to the cresta is a deep-staining accessory structure that extends longitudinally from the blepharoplast. This structure is club-shaped, and is a little longer than the cresta. Its terminal portion is greatly enlarged; the stem tapers to a slender proximal portion. Proximally it runs parallel to the anteromedial edge of the cresta to meet the blepharoplast at the same point. The enlarged end is curved peripherally, often like the head of a golf club, and usually is situated within the ring close to the nuclear membrane (pl. 14, fig. 20). This clavate crestal accessory is a unique feature of *Caduceia monile.*

The trunk of the axostyle, which is moderately developed and is filamentous posteriorly, is like that of *Caduceia bugnioni* (pl. 13, fig. 18). In the protuberance anterior to the nucleus there is a membranous sheet which is a portion of the capitulum (pl. 14, fig. 22). It stains well and can be clearly traced. On the side opposite the cresta it passes forward from the edge of the broadest part of the nucleus into the protuberance, and is expanded ventrally into the papilla. On the crestal side it similarly passes forward, occupying the full breadth of the protuberance. It is situated entirely on the left side of the granules and other anterior organelles. At the anterior end of the protuberance it is bent to the left, forming a cap. Between this stainable cap and the ring a prominent clear area is visible in specimens that are viewed from the left side.

The chromatic shield (pl. 14, figs. 20, 22) is situated on the crestal side alongside of, and anterior to, the nucleus. In heavily stained material it appears dense, and in optical section is shaped somewhat like a moderate-sized *Devescovina* cresta. What would correspond, then, to the posteromedial edge is applied for its full length to the nuclear membrane or capitulum, passing posteriorly about half the length of the nucleus. The anteromedial edge is entirely anterior to the nucleus, and the lateral edge is free of this. The analogy to a cresta does not indicate the thickness which this chromatic shield possesses. In well-differentiated material the chromatic shield reveals itself as an aggregation of small, closely packed granules. It is constant in occurrence, relative size, and shape in *Caduceia monile* which is not undergoing division.

The parabasal body is spiraled closely around the trunk of the axostyle in from 5 to 15 turns, averaging about 10. The majority of fully developed specimens have 9 to 12 turns. The longitudinal part passes along the nucleus to its anterior end, then turns back sharply in a bar that is about half the length of the nucleus. At the apex of the bend the parabasal is elevated in a blunt protuberance (pl. 14, fig. 21). The chromophile element of the parabasal is a stout cord or band in the spiral portion, where it follows one edge (pl. 14, fig. 20). It separates from the longitudinal limb at some distance from the anterior end, and proceeds directly to meet the blepharoplast just posterior to the point of attachment of the cresta (fig. B, 1).

Short rod-shaped microörganisms often occur in the cytoplasm, frequently aggregated in the region of the nucleus (pl. 13, fig. 18). These will be described later, in the section on endozoic organisms.

The surface of the entire body, including the anterior protuberance and papilla, is covered densely with short spirochaetes, in size and distribution like those on *Caduceia bugnioni* (pl. 13, fig. 18) The adherent rods characteristic of that species are absent, however, from the surface of *C. monile.*

### **Caduceia kalshoveni** sp. nov.

(Pl. 12, fig. 14; pl. 13, figs. 15–17; fig. A, 3; fig. B, 1)

*Type host.*—*Neotermes dalbergiae* Kalshoven. Java.

T-4568. Bandjar, West Java. (Syntype slide TP-3231:2.)

T-4532, 4541, 4570. Bandjar, West Java. (Homosyntype slides TP-3232:3, 4.)

*Diagnosis.*—Length 88 (35–130)μ; width 58 (18–89)μ; slender ring in anterior part of body, diameter in average-sized specimens 13–15μ; trailing flagellum a slender cord, shorter than body; cresta relatively very small, subtriangular, length about 1–2μ; parabasal body coiled tightly around trunk of axostyle, successive turns very close together, number 3–20, usually 11–14 in average-sized individuals; chromatic shield absent; nucleus 9 (7–12) by 5.5 (4.5–8)μ; short spirochaetes forming a dense coat over entire surface; *Fusiformis*-like rods absent.

On one slide numerous unusually small specimens of this species were found, accompanied by but few larger ones. They corresponded in every respect to the larger forms, but had an average size of only 48 by 29μ, and possessed a parabasal body with few turns. Other slides made from the same colony of termites had larger flagellates. These numerous small ones were omitted in preparing the average measurements, as it was some unusual factor which resulted in an abundance of such small specimens.

There are marked differences between this species and *Caduceia monile*, though the two are more closely related to each other than to other species of *Caduceia.*

The anterior part of the body merges into the relatively small papilla, and there is no sharply marked-off protuberance as in *Caduceia monile.* In the anterior part there is a ring (pl. 13, figs. 15, 16), but this is unlike that present at the base of the papilla of *C. monile.* It is better defined in iron-haematoxylin material fixed in Hollande's and Flemming's fluids than in that fixed in Schaudinn's fluid. It is slender, whereas that of *C. monile* is stout, and it is much wider. The diameter of the ring in specimens of average size is 12–15μ, whereas in *C. monile* it is 7–10μ.

The more posterior of the roots of the anterior flagella ends at a large irregular granule (pl. 12, fig. 14). This is connected by a fine fibril to the blepharoplast group of several closely approximated granules. To this blepharoplast group the anterior flagellar root passes; and with it the cresta, trailing flagellum, and parabasal body connect. The cresta (pl. 12, fig. 14; fig. A, 3) in relation to the large size of the body is almost vestigial. Without consideration of the comparative morphology of the genus it would be easy to overlook it. It has the usual subtriangular form, with the posteromedial margin concave, and there is no crestal accessory. It does not resemble the unique cresta of *Caduceia monile.*

The anterior part of the parabasal body terminates in a bluntly rounded end usually almost on a level with the anterior end of the nucleus, but not applied to the nuclear membrane (pl. 12, fig. 14; fig. A, 3). Along the inner edge of the entire coiled part of the parabasal body is the stout, deep-staining chromophile element. This element is present, though not so stout, along the longitudinal part; and it continues beyond its end to the blepharoplast.

The unusually small individuals which were numerous on one slide had 2–5, usually 3 or 4, turns in the parabasal spiral. Generally, however, there are more turns than this, 11–14 being most frequent. The maximum number observed was 20, which is the greatest number that has been seen in any flagellate.

Extending anteriorly from the nucleus into the papilla is a narrow, concave membrane which is evidently an extension of the capitulum of the axostyle (pl. 12, fig. 14). Beginning near the longitudinal part of the parabasal body, there are two parallel oblique filaments (pl. 13, fig. 16) which probably represent edges of the capitular membrane.

The ectoplasm, which has a thickness of about 2$\mu$, has a very different character from the endoplasm. This is especially evident in sections (pl. 13, fig. 17). It appears homogeneous, without granules or vacuoles, and takes a brownish stain in Schaudinn–iron-haematoxylin material. It seems denser and is more deeply stained than the chromophobe substance of the parabasal body in the same preparations. The endoplasm is clear, alveolar, and contains numerous granules and ingested wood particles.

Short spirochaetes form a dense investment over the entire surface (pl. 12, fig. 14), especially on the papilla. No imbedded basal granulelike ends such as those described in *Pseudodevescovina uniflagellata* (Kirby, 1936) were observed.

### **Caduceia pruvoti** (Duboscq and Grassé) comb. nov.

(Fig. C, 1, 2)

*Devescovina pruvoti* Duboscq and Grassé, 1929, *partim,* Arch. Zool. exp. gén., 68, Notes et Revue: 8, figs. 3, 4.

*Type host.*—*Kalotermes* sp. Lifou, Loyalty Islands.

*Diagnosis.*—Maximum length 75$\mu$, width 36$\mu$; form stout, rounded posteriorly; anterior flagella short, trailing flagellum cord-formed, about body length; cresta slender, length in figures 8–11$\mu$; parabasal body long, coiled around axostyle 12 times in the original figure; chromatic shield probably present; nucleus elongated, tapered anteriorly and pointed posteriorly; surface covered with a dense investment of short spirochaetes.

In preparations from an undetermined species of *Kalotermes,* Duboscq and Grassé recorded a species of *Trichomonas* and *Devescovina pruvoti* sp. nov. In agreement with their usual practice, they described, as stages in the life cycle of *Devescovina pruvoti, Trimitus* forms, young stages, and large forms. The first is *Tricercomitus,* probably *T. divergens.* The second probably includes *Foaina* and *Devescovina,* some having a stout bacilliform parabasal, and others, larger in size, having a coiled parabasal. The description of the large forms is more complete, and since they are the forms regarded as typical of *Devescovina pruvoti,* and the only ones that could be identified from the descriptions with flagellates of other hosts, the name *pruvoti* may be used for them. It seems to me that they belong to the genus *Caduceia,* along with *C. bugnioni* and the other species described in this paper.

The three anterior flagella are figured (fig. C, 1) as about half the length of the body, and the cordlike trailing flagellum, about body length. The cresta is slender, tapers posteriorly, and, according to the magnification given, is about 8μ long in one figure and 11μ in the other. The trunk of the axostyle is moderately slender and tapers to a filamentous posterior end within the cytoplasm. In one figure (fig. C, 2) there are two anterior granules, one receiving the cresta and trailing flagellum and the other the three anterior flagella. This resembles the situation in *Caduceia bugnioni* and *C. monile*, except that in them one anterior flagellum meets the other granule. One could, however, easily misinterpret this arrangement in inadequate material.

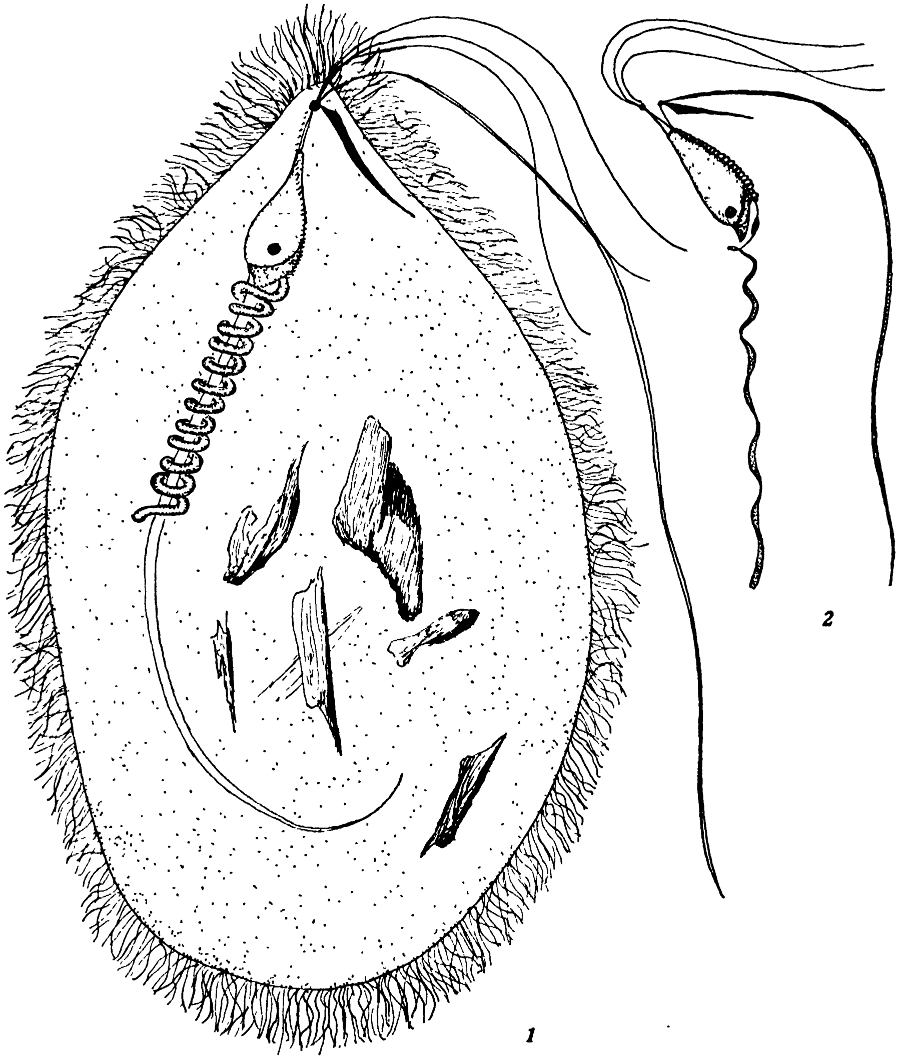

Fig. C. *Caduceia pruvoti* (Duboscq and Grassé) from *Kalotermes* sp. of the Loyalty Islands. 1. Individual covered with spirochaetes. Axostyle tapered posteriorly and enclosed in cytosome as in other species of the genus. × 2000. 2. Nucleus, flagella, cresta, parabasal apparatus. The close spiral alongside the nucleus, supposed by the authors to be the anterior part of the parabasal, is probably part of the chromatic shield. × 1330. (After Duboscq and Grassé, 1929.)

The parabasal body is similar to that of *Caduceia monile*. In Duboscq and Grassé's figure III (fig. C, 1) it is coiled in twelve close turns around the axostyle. The parabasal thread at one edge was distinguished by them as the chromophile substance, the remainder as chromophobe. However, if I correctly understand their brief description, they believed the chromophile substance to be on the external side of the spiral, whereas in all devescovinids studied in preparation of this monograph the chromophile element is on the anterior or inner side.

The anterior part of the parabasal body of *Caduceia pruvoti* is, according to the description, unique among known devescovinids (fig. C, 2). It appears "comme un fine spire serrée, d'environ 25 tours, formée par un filament éosinophile dans lequel sont inclus des grain sidérophiles, parfois seuls visibles." In *C. bugnioni* and *C. monile* the anterior part of the parabasal is bordered by a straight parabasal filament, which separates from it, and nothing like the fine, close spiral of about 25 turns exists. The anterior part of the parabasal body passes close to one edge of the chromatic shield, which shows clearly in certain preparations in which the longitudinal part of the parabasal is not visible. The chromatic shield consists of numerous small siderophile granules. Duboscq and Grassé stated that within the spiral there are enclosed such granules, which sometimes alone are visible. This fact, together with the bizarre nature of the supposed anterior part of the parabasal they described, leads me to believe that they misinterpreted an edge view of the chromatic shield, and did not see the anterior part of the parabasal body.

The nucleus is elongated longitudinally and contains a nucleolus. It is tapered anteriorly, to an end said to be truncated. There is an achromatic prolongation to the blepharoplast, which Duboscq and Grassé believed to be comparable to the suspensorial lamella of Janicki, and to represent an extension of the axostyle. Possibly this is the anterior extension of the chromatic shield, as in *Caduceia monile.* No suspensorial lamella has been observed by me in the species of *Caduceia* studied, and the anterior part of the capitulum does not have the narrow band form shown for this structure.

Duboscq and Grassé stated that the adherent spirochaetes resemble *Treponema hilli.*

## GENUS MACROTRICHOMONAS GRASSI

### **Macrotrichomonas** Grassi

*Macrotrichomonas* Grassi, 1917, Mem. R. Accad. Lincei, (5) 12:376 (type species *M. pulchra* Grassi).—Kirby, 1938, Univ. Calif. Publ. Zoöl., 43:15.

*Gigantomonas* Connell, 1932, *partim,* Univ. Calif. Publ. Zoöl., 37:180 (not *Gigantomonas* Dogiel).

*Diagnosis.*—Devescovinids of large size, known species 26–91$\mu$ long, averaging 43–68$\mu$; 10–49$\mu$ wide, averaging 19–38$\mu$; three anterior flagella; trailing flagellum well developed, band-formed in some species, usually about 1–1½ times length of body; cresta developed into a broad internal membrane, 21–86$\mu$ long, reaching from nucleus to periphery of body; parabasal body coiled closely around the trunk of the axostyle 1–13 times, branched in one species; capitulum moderately developed, often with arm, extended posteriad, originating in anterior part; trunk of axostyle stout anteriorly, tapering but not reduced to a filament nor extended in a filament, no terminal enlargement, end generally pointed, usually projecting a certain distance; nucleus of the *Devescovina* type, larger and smaller chromatic granules with or without a space under the nuclear membrane, longer axis longitudinal and blepharoplast anterior; no regularly adherent rod-shaped microörganisms; long spirochaetes present on anterior and posterior ends of some species.

## TAXONOMY AND DISTRIBUTION

In the appendix to the paper in which he described *Macrotrichomonas pulchra,* Grassi stated that he had seen a review of the paper by Dogiel (1916) on the Tetramitidae from *Hodotermes mossambicus,* and that it seemed from it that *Macrotrichomonas* (there written in error "*Macrotrichonympha*") should be synonymous with *Gigantomonas* Dogiel. He was unable to obtain the original paper. (Evidently, as the dates indicate, the review was seen and the note was added shortly before the paper was published.) After a careful study of the papers of Dogiel and Grassi, Connell (1932) concurred in this opinion. He maintained that the flagellates described as *Gigantomonas herculea* by Dogiel, *Macrotrichomonas pulchra* by Grassi, and *Gigantomonas lighti* by himself are all congeneric; and in support of this opinion he gave detailed comparisons of the morphological characteristics of the three species. He was, however, unable to examine specimens of *G. herculea.* I have been able to study both living material and preparations of Dogiel's flagellate, and, as stated before (1937*a*), I do not agree with the proposed synonymy. *G. herculea* should not be included in the subfamily Devescovininae, as will be made clear in a detailed description of the species to be published later.

Mesnil's review of Dogiel's paper, published in the Bulletin de l'Institut Pasteur for December 15, 1917, actually presented little evidence for the conclusion Grassi drew; for it mentioned only general characteristics, such as four anterior flagella (one of these is really the trailing flagellum), an undulating membrane without a chromatic basis (the undulating membrane referred to there is the cresta), and an axostyle. There is in *Gigantomonas* a large cresta comparable to that of *Macrotrichomonas,* though in detail unlike that of any known species of the latter genus. Adherent to the edge of the cresta, though separated in many preparations, as apparently had happened in those used for study by Dogiel, is a cordlike trailing flagellum. Connell correctly understood the nature and homology of the undulatory cresta in *Gigantomonas* and devescovinid flagellates. In addition, however, he recognized both the posteriorly directed flagellum and, somewhat equivocally, an undulating membrane. The flagellum, he stated, follows the outer margin of the undulating membrane, the base of which is fused to the external margin of the cresta. As is discussed elsewhere in this paper, however, the trailing flagellum, whether cordlike or ribbonlike, is not homologous with a trichomonad undulating membrane; and there is no membrane between that flagellum and the cresta. Connell based his conclusion that the species *herculea, pulchra,* and *lighti* are congeneric on the statement that "three species of Devescovininae are known in which the large posteriorly directed flagellum is fused to the external margin of the cresta at the pellicle, forming an undulating membrane." In the relationship of trailing flagellum and cresta, however, the three flagellates are in agreement with all Devescovininae.

There are important differences that Connell failed to stress between *Gigantomonas herculea* and the flagellates which I place in the genus *Macrotrichomonas.* One of these is the absence in *Gigantomonas* of the parabasal body, a structure prominent in all Devescovininae. Connell thought that it was probably present, although Dogiel had failed to describe it, but in fact there is no parabasal body. The body of *Gigantomonas* is much more labile than that of *Macrotrichomonas.* In preparations it is almost invariably greatly altered in shape; whereas normal-shaped specimens of *Macrotrichomonas* are easy to obtain on slides. Connell argued the probability that *Myxomonas polymorpha* is synonymous with *Gigantomonas herculea,* representing certain mitotic phases. This is so, but the consequent life-history changes are altogether unlike anything that occurs in *Macrotrichomonas* or other Devescovininae. Division stages occur also in the typical *Gigantomonas* form, and these do not differ essentially from division stages of *Macrotrichomonas.* There also develop the large amoeboid forms, the appearance and locomotion of which are like those of amoebae; these often possess two nuclei connected by a paradesmose. Various stages in reorganization of the mastigont structures may be seen in them, and much foreign material is ingested. The amoeboid forms resemble no division stages of *Macrotrichomonas,* are in no sense degenerate forms, and usually outnumber the typical *Gigantomonas* forms. There is, furthermore, no isolation of a single type in a termite; and the forms are not to be explained on the basis of the occurrence of mitotic flares, as Connell suggested and as I thought possible before seeing the material.

The seven species of *Macrotrichomonas* occur in 23 hosts in all, and these are widespread geographically. Investigation has not discovered more than one in a host. In 13 of the hosts the species is *M. pulchra,* and the termites have so wide a distribution that the flagellate is evidently a very ancient form. It has been found in Africa, Australia, the Philippine Islands, the Fiji Islands, Ceylon, Java, and Central America. All the termites belong to the genus *Glyptotermes.* The other species are in conspicuous contrast to *M. pulchra* in their limitation to one host or a small number of closely related hosts. Two of them, *M. unguis* and *M. ramosa,* have evidently originated from *M. pulchra* by single differences; these also occur in species of *Glyptotermes.* The remaining four species are each unique in various characteristics. They occur in a species each of *Kalotermes* s. str., *Procryptotermes,* and *Paraneotermes,* and in the four species of *Calcaritermes* that have been examined.

## GENERAL MORPHOLOGY

In *Macrotrichomonas* the cresta has undergone an enormous development. It has become a large intracytoplasmic membranous structure, which is the most conspicuous feature of the flagellates stained so as to show it clearly. The anteromedial edge is elongated to extend from the blepharoplast, which is situated at a variable distance anterior to the nucleus, to a point usually a short distance posterior to the nucleus. Unlike most other crestas, this edge is applied closely to the capitulum of the axostyle (pl. 18, fig. 35). Connell believed that in *M. lighti* it is firmly fused to the axostyle. Although the position of the cresta remains constant in ordinary vegetative forms, in division stages the cresta and axostyle are entirely separate. The length of the external edge of the cresta usually exceeds half the length of the body. This in itself is not unusual, as there are crestas more than half body-length in certain species of *Foaina* and *Metadevescovina.* These species, however, are relatively small, and the crestas relatively narrow. Only in *Macrotrichomonas* is the cresta broadened to a membrane reaching in its anterior part from almost the midline of the body to its edge; and among the Devescovininae, *Gigantomonas* being omitted, only in that genus is large body size accompanied by a relatively great increase in crestal size. The external part of the cresta is more or less waved in undulatory folds (pl. 15, fig. 25). In the cresta of *M. lighti,* Connell (1932) and I as well have observed vigorous intracytoplasmic undulatory movements. Undulatory activity is described also in the cresta of *M. restis* (p. 127).

In *Macrotrichomonas pulchra,* Grassi (1917) described a thin undulating membrane attached along the external side of the cresta, forming a free flagellum posteriorly. This is a band, which is shown detached in some of his figures. Connell also described an undulating membrane in *M. lighti,* stating that the stout fourth flagellum borders its outer margin, and that its base is fused to the external border of the cresta. Kirby (1938*a*) described in *M. pulchra* a ribbon-formed trailing flagellum paralleling the edge of the cresta and probably normally adherent by an edge that stains more deeply than the other (pl. 15, fig. 25). That this is a broadened flagellum, and not an undulating membrane bordered by a marginal flagellum, is indicated by its ready detachment and its structural details. Correct interpretation is facilitated by comparison with the situation in other devescovinids. In both *M. lighti* and *M. pulchra* the trailing flagellum is band-formed, but in *M. restis* (pl. 19, fig. 50) it is a cord, and confusion with an undulating membrane is not likely.

In contrast to the cresta, the parabasal body and axostyle in *Macrotrichomonas* have remained comparatively simple. The parabasal body reaches to a position close to the blepharoplast (pl. 16, fig. 27), with only a slight separation of the filament, unlike the situation in *Devescovina* and many other forms. There is usually no marked extension of the anterior end, and the close coiling around the trunk of the axostyle is of the *Devescovina* type. The only unusual feature of the parabasal body is the limited branching in *M. ramosa* (pl. 18, figs. 37–45).

The trunk of the axostyle is of the *Devescovina* type, but it does not become filamentous within the cytoplasm. In its form it resembles the axostyles of *D. parasoma, D. robusta,* and *D. vestita.* It differs from axostyles of the *Foaina-Metadevescovina* type in never having an enlarged posterior cusp. It tapers posteriorly and usually projects from the posterior end for a certain distance. The end is often sharpened rather abruptly. Connell's statement that the sheath of the axostyle is fibrillar is discussed in the account of *M. lighti* (p. 132).

The capitulum does not have the elaborate membranous expansion of some devescovinids. There is, however, in several species an armlike capitular appendage, arising anteriorly and extending posteriad toward the beginning of the parabasal spiral. A similar structure was described in *Pseudodevescovina uniflagellata* (Kirby, 1936).

The elongation of the nucleus is in a longitudinal direction, as in *Devescovina,* and the blepharoplasts are anterior to the nucleus. Usually the nucleus agrees with that of *Devescovina* in the presence of numerous granules and masses of readily stainable material. A clear space between the chromatin mass and the nuclear membrane appears in some material, as it does under the influence of fixation in *Devescovina,* but it is not apparent in the best-fixed material.

Spirochaetes, many of which have a length of 15–20μ, are adherent to parts of the body of most species of *Macrotrichomonas.* They appear to be absent from *M. lighti* and *M. restis,* and are not present on all individuals of other species, but in their type and distribution they are often characteristic. Most of the species have a tuft of a few spirochaetes on the papilla, and often spirochaetes are more or less numerous on the posterior part of the body. The rods adherent to *M. virgosa* are unusual in their type and their relationship to the body of the flagellate. They have already been discussed and figured by me (1941), and are described in detail below (p. 130).

### KEY TO THE SPECIES OF MACROTRICHOMONAS

1. Posteromedial edge of cresta equal to or exceeding the anteromedial edge in length.....2
   Posteromedial edge of cresta much shorter than the anteromedial edge.......*M. procera*
2. Medial edges of cresta reinforced by riblike thickenings, each with a bulbous enlargement at the angle between the medial edges........................*M. lighti*
   Medial edges of cresta without such marked bulbous thickenings..................3
3. Trailing flagellum cord-formed..........................................4
   Trailing flagellum band-formed..........................................5
4. Inner angle of cresta anterior to posterior end of nucleus; parabasal spiral beginning immediately posterior to nucleus; rods adherent by one end to posterior part of body..........................................*M. virgosa*
   Inner angle of cresta several microns posterior to the posterior end of nucleus; parabasal spiral beginning several microns posterior to nucleus; no adherent rods..........................................*M. restis*
5. Parabasal body with one to three rami at the beginning of the spiral in the majority of specimens..........................................*M. ramosa*
   Parabasal body only exceptionally branched..................................6
6. Cresta with a rectangular, shelflike extension from the posterior part of the anteromedial edge..........................................*M. unguis*
   Cresta without this extension..........................................*M. pulchra*

## MORPHOLOGY AND DIAGNOSIS OF SPECIES OF MACROTRICHOMONAS

### Macrotrichomonas pulchra Grassi

(Pl. 15, figs. 24–26; pl. 16, figs. 27–29; fig. D)

*Macrotrichomonas pulchra* Grassi, 1917, Mem. R. Accad. Lincei, (5) 12:50, pl. 9, figs. 1:12.—Kirby, 1938, Univ. Calif. Publ. Zoöl., 43:16, pl. 3, figs. 17–19; pl. 4, figs. 20–27; pl. 5, figs. 28–38; pl. 6, figs. 39–41.

*Gigantomonas pulchra* (Grassi). Connell, 1932, Univ. Calif. Publ. Zoöl., 37:180.

*Gigantomonas pulchra.* Grassé, 1937, C.r. Soc. Biol., 125:918.

*Type host.—Glyptotermes parvulus* Sjöstedt. Gold Coast.
T-301. (Silvestri.) (Xenosyntype slides TP-318:1, 2.)

*Additional hosts*

*Glyptotermes ceylonicus* Holmgren. Ceylon.
T-314. (Cleveland-Collier.) (Homosyntype slide TP-265:5.)
*Glyptotermes contracticornis* (Snyder). Costa Rica. (Formerly referred to by me as *Kalotermes*. Assignment to *Glyptotermes* by Emerson, *in litt.*)
T-132. Cartago. (Homosyntype slides TP-72:15, 12, 14, 19.)
*Glyptotermes dubius* Mjoberg. Australia.
T-511. (Hill 3232.) Ravenhoe, Queensland. (Homosyntype slides TP-511:2, 50, 99.)
*Glyptotermes perangustus* Hill. Australia.
T-512. (Cleveland-Hill.) Sydney. (Homosyntype slide TP-512:7.)
*Glyptotermes iridipennis* Froggatt. Australia.
T-510. (Cleveland-Hill.) N.S.W., about 150 miles north of Sydney. (Homosyntype slides TP-510:2, 4, 41, 13.)
*Glyptotermes montanus* Kemner. Java.
T-324. (Cleveland-Collier.) (Homosyntype slide TP-262:11.)
*Glyptotermes neotuberculatus* Hill. Australia.
T-513. (Hill 3194.) Australian Capital Territory. (Homosyntype slide TP-513:3.)
*Glyptotermes taveuniensis* Hill. Fiji Islands.
T-515. (Hill 4065. Cleveland.) (Homosyntype slides TP-515:9, 13, 18, 5.)
*Glyptotermes* sp. nov. Uganda.
T-2072. Near Kampala. (Homosyntype slides TP-2018:13, 17; TP-2023:20.)
*Glyptotermes* sp. nov. Belgian Congo.
T-3018. Near Rutchuru. (Homosyntype slide TP-2035:8.)
*Glyptotermes* sp. nov. Ruanda-Urundi.
T-3022. Kakitumba. (Homosyntype slide TP-2037:13.)
*Glyptotermes* sp. nov. Philippines.
T-4601. (Light 1744.) Mount Maquiling, Luzon. (Homosyntype slide TP-3285:20.)

*Diagnosis.*—(From type host): length 67 (44–91)μ; width 32 (21–41)μ; three anterior flagella; trailing flagellum band-formed, cresta large, inner part uniformly dense, outer part undulated, anteromedial edge about 14μ, posteromedial edge concave, in straight line about 19μ long, paracrestal filament extending along and a short distance beyond anteromedial edge; parabasal body coiled closely 4 or 5, up to 10 times; capitulum of axostyle bordered ventrally by suspensorial lamella; trunk of axostyle tapering posteriorly without filamentous end or cusp, bluntly pointed end often projecting a short distance; nucleus averaging 9.6 by 7.7μ; a few long spirochaetes usually adherent in the region of the papilla. (From *Glyptotermes contracticornis*): length 57 (42–83)μ; width 25 (16–33)μ; distance between anterior end of nucleus and anterior end of body 7 (5–9)μ; trailing flagellum 1.5–1.8μ broad, inner part smooth, stainable, outer part clear, undulated; length of cresta 25–35μ, greatest breadth 5–10μ, anteromedial edge about 14–18μ, posteromedial edge about 17–26μ; parabasal body coiled closely 2–9, one 13, most often 3–4 times; suspensorial lamella and bent nuclear rhizoplast present; nucleus 8.3 (7.5–10) by 6.4 (5–7.5)μ; spirochaetes 15–20μ long sometimes present on anterior and posterior ends. (From *Glyptotermes montanus*): length 49 (36–68)μ; width 23 (16–31)μ; cresta length 25–34μ, width 5–9μ. (From *Glyptotermes ceylonicus*): length 52 (37–66)μ; width 26 (19–39)μ; cresta length 21–28μ, width 5–8.5μ; nucleus 8.3 (7.4–9) by 5.8 (5–6.4)μ; no adherent spirochaetes seen. (From *Glyptotermes* sp. nov. T-2072): length 58 (40–78)μ; width 34.5 (23–49)μ; length of trailing flagellum 85–105μ; width often 2–2.5μ; cresta length 34 (24–41)μ, anteromedial edge 17 (15–19)μ; turns of parabasal body 4.5 (2.5–7); nucleus 8.4 (7–10) by 6 (5–7)μ; spirochaetes often present on anterior end. (From *Glyptotermes iridipennis*): length 48 (35–59)μ; width 21.5 (17–29)μ; length of trailing flagellum 100–118μ, width about 2μ; cresta length 27.5 (22–31)μ, anteromedial edge 16.5 (14–19)μ; parabasal turns 4 (2.75–5.5); nucleus 7.4 (6.3–8.6) by 5.3 (4.2–6.3)μ.

***Macrotrichomonas pulchra*** was abundant in all material of *Glyptotermes iridipennis* collected by Cleveland in Australia in 1938; but it was absent from the same species of termite sent to me by Mr. F. G. Holdaway and Mr. G. F. Hill in 1934, and it was not reported from the host species by Duboscq and Grassé (1927). Cleveland's smears were made in Australia, whereas the other termites had been shipped for a long distance. Possibly these devescovinids had died in transit, although the other flagellates of the faunule survived.

Since my earlier account of the species was published (1938*a*), some excellent additional material has become available, so that a revised and supplemented description can be given.

The arrangement of the blepharoplast and associated granules has been studied in great detail, and it is believed that the following description is exact and complete. It is in essential agreement with the earlier account, but adds certain details. Very distinct in all suitably stained material are the enlargements of the two roots of the three anterior flagella and, posterior to these, a relatively large granule (pl. 16, figs. 27–29). Anterior to the large granule and directly connected to it is a small granule which is the center of the fibrillar system. In heavily stained Flemming-fixed preparations of *Glyptotermes* sp. nov. T-2072 from Uganda the small granule appears very definite and is of moderate size; in Schaudinn-fixed specimens it is often minute, as was stated in 1938, and sometimes can hardly be seen at all.

The more anterior of the flagellar roots, which divides into two flagella, is the stouter. It ends in a club-shaped enlargement a short distance from the central granule, to which it is connected by a fine filament. In the earlier description it was stated that the other root also ends in a definite granule which is connected to the central granule. This description, however, is not exact. The flagellar root itself runs directly to the central granule, and the apparent enlargement is an elongated structure, rodlike or subtriangular, which lies alongside the root (pl. 16, fig. 29). In iron-haematoxylin-stained material it is separated from the root by a narrow clear space. This structure has been observed in both African and Australian specimens.

The cresta and trailing flagellum end separately a short distance from the central granule, each in a small granule (pl. 16, fig. 29). They are probably each connected by a fine filament to the central granule. The earlier account was incorrect in stating that there was a single granule common to the ends of the cresta and trailing flagellum; there is no granule, other than the central blepharoplast, to which these are both connected.

The large granule immediately posterior to the central granule often has an irregular shape and is variable in size. In many specimens examined it is double, the two parts being closely approximated and often unequal in size.

It was stated in 1938 that to this large granule are connected the rhizoplast and parabasal body. The nuclear rhizoplast meets it in its middle or anterior part on the side away from the cresta, but it cannot be determined whether or not the rhizoplast continues to the central granule. The parabasal filament meets it on the other side or near the posterior end; possibly it continues against it to the central granule.

In suitably stained material the nuclear rhizoplast is always conspicuous (pl. 16, figs. 28, 29). Posteriorly it comes in contact with the nuclear membrane near the side opposite the cresta, not the anterior end, and it runs along the nuclear membrane for a certain distance. It has not been possible to trace this part against the nuclear membrane for its whole length, as it is obscured by the chromatin mass, which stains heavily by the methods necessary to demonstrate the rhizoplast. In its anterior part it usually passes transversely or obliquely for a distance of about 3$\mu$, approaching close to the suspensorial lamella (pl. 16, fig. 28). Then it bends posteriorly and passes straight to the nuclear membrane. The rhizoplast often appears as a narrow band instead of a simple filament.

In differential stainability the cresta is comparable to the trailing flagellum. The outer edge appears as a well-defined filament, similar to that at the margin of the flagellum. When suitably differentiated, the outer part of the cresta is clear. There is a rather sharp separation of the clear and the stainable parts (pl. 15, fig. 25). The inner part stains more or less deeply, especially toward the inner edge, but there is no sharply defined thickened area. The undulations of the cresta involve only the outer clear part; the stainable part is rather flat.

Living material from *Glyptotermes* T-2072 was observed in East Africa. There was continuous vigorous undulatory activity of the trailing flagellum. Movement was not observed in the cresta; and in some specimens it was clear that the trailing flagellum was not attached, and that it undulated alone. Often it seemed to adhere to, or slide over, the body surface. There was often an irregular disturbance in the cytoplasm, but this was the result of the general body activity, not of any activity of the cresta. Likewise, in the flagellates from *Glyptotermes taveuniensis* no motility of the cresta was observed, but more study of *Macrotrichomonas pulchra* is necessary in regard to that point. In the flagellate from the latter host a repeated arrest of all movement for a short period was noted, activity being resumed after a minute or so.

The paracrestal filament has been seen in suitably prepared material from all hosts, including *Glyptotermes ceylonicus,* in which it was reported before (1938*a*) that it had not been observed. Anteriorly it is connected direct to the central blepharoplast (pl. 16, fig. 28), and it runs parallel to the anteromedial edge of the cresta, being separated from it by a narrow clear space constant in width. It becomes stouter along the posterior part of this edge of the cresta, and beyond the cresta it expands to a rather stout strücture several microns in length, which is enclosed within the parabasal spiral.

The chromophile element of the parabasal apparatus is broadened in the coiled part; often it is a band (pl. 16, fig. 27). In certain Flemming-Regaud material it appeared particularly stout, but often it is no stouter in this than in Schaudinn-fixed material, and may even appear more slender. It has been followed more clearly along the outer edge of the longitudinal part than was possible in the Central American material. When it approaches the posterior granule of the blepharoplast group it separates from the other parabasal substance, which continues farther (pl. 16, figs. 27–29). Beyond the point of closest proximity to the blepharoplast the parabasal body is often bent in the form of a golf club. The part beyond the bend has a length of about 2μ and it varies in thickness. Often it is little if any larger than the rest of the longitudinal limb, but frequently there is considerable thickening (pl. 15, fig. 24).

The capitulum spreads on the right and ventral sides of the nucleus and forward into the papilla. Close to the ventral side of the body is the suspensorial lamella (pl. 15, fig. 25), which extends from the papilla region, without definite connections with the blepharoplast, and passes along the ventral border of the capitulum to end against the nuclear membrane. It appears deeply stained in edge view, and renders the position of the ventral edge of the capitulum very conspicuous for most of its length (pl. 16, fig. 28).

Near the posterior end of the nucleus the sheath of the axostyle, before extending into the capitulum, is folded posteriorly, so that in optical section there is the appearance of a posteriorly directed tooth at the posteroventral part of the nucleus (pl. 16, fig. 28). The shape of the nucleus was observed in one specimen to be altered to correspond to the fold of the axostyle, but that is not characteristic. The posterior fold extends partway around the nucleus, but not to the dorsal side.

When the cresta is on the observer's right, there appear above the nucleus two lines passing from the papillar part of the capitulum, at the anterior left, to end against the nuclear membrane at the posterior right. Two interpretations can be given to these oblique lines. In the published account of *Macrotrichomonas pulchra* (1938*a*) it was suggested that the line to the right (the only one then seen), passing obliquely from near the cresta in the region of the granules, represented an edge of the capitulum. The capitulum, it was supposed, was folded over on this side of the nucleus. It now appears that the second interpretation is more probable, namely, that the two lines are the edges of a cylindrical capitular appendage which leaves the main part of the capitulum in the papilla and extends on the side of the nucleus opposite to it. The capitular appendage is often marked by adherent granules, though not so clearly or consistently as in *Pseudodevescovina uniflagellata.* Granules or rods adherent to the capitulum (pl. 16, fig. 27) are frequently present in *M. pulchra* from various hosts.

The trunk of the axostyle (pl. 15, fig. 25) is never expanded into an enlarged posterior cusp, nor does it become filamentous. A truncate or rounded end is typical of it in many specimens of *Macrotrichomonas pulchra,* but in other specimens it is sharpened to a blunt point. A short projection, generally of not more than 3 or 4μ, and often less, is characteristic. The end of the axostyle is completely enclosed in the cytoplasm more often than in *Foaina* and *Metadevescovina;* but it is not like *Devescovina* and *Caduceia,* in which enclosure is usual. Around the trunk of the axostyle just prior to the projection from the body there is often evident a deep-staining, collarlike thickening. Anterior to this there is often a more or less dense aggregation of granules of the same type as those present elsewhere in the cytoplasm. The posterior part of the sheath of the axostyle, for a distance of several microns within the cytoplasm as well as the projecting part, often stains more deeply with iron-haematoxylin than do the more anterior parts.

The longer axis of the nucleus is in line with the trunk of the axostyle. The nucleus is broadly ellipsoidal in form, except that it is often extended posteriorly in a short, blunt projection. The chromatin mass is often extended into this projection, with no break in continuity. There is no separate deep-staining cone in the trunk of the axostyle posterior to the nucleus. In material well fixed in either Schaudinn's or Flemming's fluids the chromatin mass fills the interior. Especially in the Central American and African material, a space of variable breadth appeared around it. The space was infrequent in the Australian specimens. In the presence of this clear space, however, the nucleus is at times like that of *Devescovina* rather than that of *Foaina* and *Metadevescovina*. When the chromatin mass of *Macrotrichomonas pulchra* is drawn away from the membrane, numerous granules often occur in the resulting space.

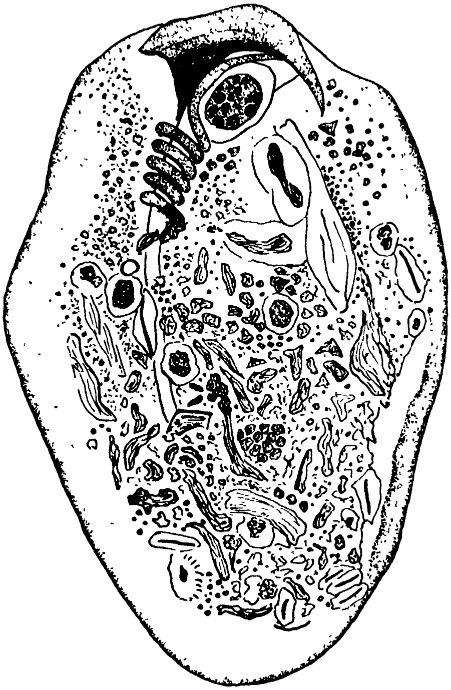

Fig. D. *Macrotrichomonas pulchra* Grassi from *Glyptotermes parvulus*. Cytoplasmic inclusions, mostly particles of wood. × 1155.

There is a spherical peripheral nucleolus of moderate or large size (pl. 16, fig. 27), and there are abundant chromatin granules of variable size and shape, some of them being larger than the nucleolus (pl. 16, fig. 28). In sufficiently differentiated material from *Glyptotermes iridipennis* there was evident a marked contrast in stainability between the nucleus of *Macrotrichomonas pulchra* and that of *Crucinympha hilli*. The nucleolus of the latter was deeply stained, but the chromatin material, consisting of small granules, was often almost or quite completely destained, whereas that of *Macrotrichomonas* on the same slide was still deeply stained.

In a small percentage of specimens from most of the hosts the nucleus was parasitized by *Nucleophaga*.

The presence of a small group of spirochaetes at the anterior end is characteristic of the species; but spirochaetes do not occur in all specimens in any host and were not found on any specimens from *Glyptotermes neotuberculatus*. They adhere to a restricted area on the papilla, posterior to the roots of the anterior flagella. A few spirochaetes of the same type adhere to the posterior end of some specimens. They are seldom abundant enough to constitute a well-defined tuft.

Usually there are no surface organisms other than the spirochaetes. Rods like those on the surface of many specimens of *Crucinympha hilli* in inconstant occurrence, distribution, and size were present on some specimens of *Macrotrichomonas pulchra* from *Glyptotermes taveuniensis* (pl. 15, fig. 26), but not on those from other hosts. In *G. iridipennis*, in which the rods are often present on *C. hilli*, they are never present on *M. pulchra*. Granules and rods are present in abundance in the cytoplasm of *M. pulchra* from various hosts. They are not all of the same type. In the Fiji material they resemble the surface rods, but probably are not the same.

### **Macrotrichomonas unguis** sp. nov.

(Pl. 16, fig. 30; pl. 17, figs. 31–34; fig. E)

*Type host.*—*Glyptotermes caudomunitis* Kemner. Java.
T-4566. Bandjar, W. Java. (Syntype slides TP-3242:23, 20, 19.)
*Additional hosts*
*Glyptotermes* sp. Java. (Possibly *caudomunitis.*)
T-4560. Bandjar. (Homosyntype slide TP-3212:3.)
*Glyptotermes minutus* Kemner. Ceylon.
T-313. (Cleveland-Collier.) (Homosyntype slide TP-264:2.)

*Diagnosis.*—(From type host): length 55 (42–72)μ; width 29 (21–37)μ; flagella, axostyle, nucleus as in *M. pulchra;* bent rod, not present in that species, between the posterior root of an anterior flagellum and the anterior angle of the rhizoplast; in the posterior part of the anteromedial edge of the cresta, which is smooth in *M. pulchra*, a rectangular, shelf-like, concave extension or unguis about 4μ in length and 2μ wide; cresta length 45 (37–52)μ; anteromedial edge 22 (17–26)μ; posteromedial edge 23.6 (21–28)μ; greatest breadth 8–11μ; parabasal turns 6 (5–9½); nucleus 7.7 (5.3–12) by 5.7 (4–7.3)μ; spirochaetes often adherent in a small tuft on the papilla, some occasionally present on the posterior part of the body. (From *Glyptotermes minutus*): length 59 (46–84)μ; width 28 (20–40)μ; cresta length 40 (36–49)μ; width 10–14μ; parabasal turns 5–7 (4–9½); nucleus 9.6 (8.3–10.7) by 6.2 (5.9–6.8)μ; no adherent microörganisms.

This species resembles *Macrotrichomonas pulchra*, but there are certain well-defined differences. The material, collected by Miss Collier in Ceylon, and originally labeled *Glyptotermes minutus*, consists of two slides, but the flagellate faunules are not alike. Both contain *Macrotrichomonas*, but they are easily distinguished as *M. pulchra* and *M. unguis;* and the faunules can readily be separated by this difference, as well as others. Since no specimens of the hosts are available, the original designation of the source of the slides as *G. minutus*, though accepted here for *M. unguis*, cannot be proved; it is incorrect for one of them. *M. pulchra* is present in *G. ceylonicus*.

In the arrangement of anterior blepharoplast granules and connections of the flagella, parabasal body, nuclear rhizoplast, and other structures, *Macrotrichomonas unguis* is similar to *M. pulchra,* with the exception discussed in the next paragraph. The larger granule immediately posterior to the central blepharoplast granule (fig. E) has not been observed to be doubled, as it sometimes is in *M. pulchra.*

*Macrotrichomonas pulchra* has a small rod-shaped body alongside the base of the posterior root of the anterior flagella (pl. 16, fig. 29). This does not extend posteriorly beyond a point a short distance anterior to the central blepharoplast, at the level of the end of the enlargement of the other root. In *M. unguis* there is also a rod along the same flagellar root; but from what would be the posterior terminus of the rod in *M. pulchra,* that in *M. unguis* continues at an angle as far as the rather sharp angle at the bend of the nuclear rhizoplast (fig. E, 1). This bent rod comes into close proximity to the flagellum anteriorly and the nuclear rhizoplast posteriorly, but probably it is directly connected to neither. The material has been studied very carefully with refer-

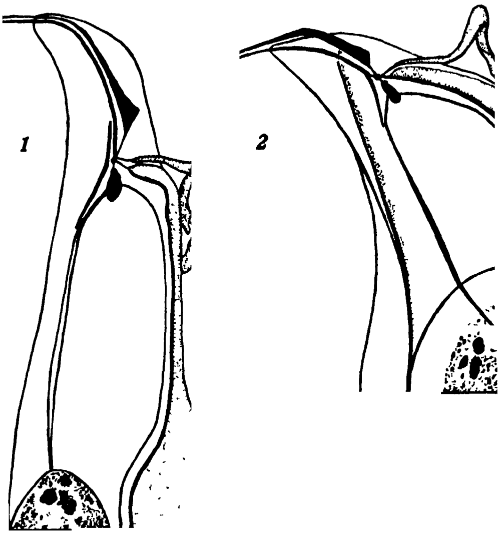

Fig. E. *Macrotrichomonas unguis* sp. nov. × 3470. 1. From *Glyptotermes minutus.* S.H. 2. From *Glyptotermes caudomunitis.* Holl. H. Diagrams giving detail of the anterior structures: the border of the capitulum; the nuclear rhizoplast; the more slender of the two roots of the anterior flagella, connected to the small central granule; the bent rod extending along the proximal part of the root and to the angle of the nuclear rhizoplast; the large granule posterior to the central granule, which is met by the nuclear rhizoplast (left) and the parabasal filament (right); the stout root of the anterior flagella, whose enlargement is considerable and which is connected by a filament to the central granule; the cresta and trailing flagellum, whose ends are also connected by slender filaments to the central granule.

ence to this structure, and a positive statement that the continuation to the angle of the rhizoplast is constant in *M. unguis* and does not exist in *M. pulchra* can be confidently made.

The capitulum is alike in the two species. In *Macrotrichomonas unguis* the oblique arm was seen clearly, and appeared broader than in *M. pulchra*. In neither species has it been possible to determine whether the arm is connected to the capitulum posteriorly, near the nucleus. No adherent rods are present on the capitulum; only a few granules were seen on occasional specimens.

The trailing flagellum (pl. 17, figs. 31, 34) was a little narrower in the material studied than is sometimes observable in *Macrotrichomonas pulchra*, not exceeding 2μ, whereas the latter reaches 2.5μ. The difference is not significant. Often the outer part of the flagellum was not undulated so much as is typical of *M. pulchra*, but occasionally it was. In the Java material there appeared a marked difference in stainability between the inner and outer parts of the flagellum, as in *M. pulchra*, but this was not evident on the one smear from *Glyptotermes minutus*.

Though there are crestas of the two species in which the size is similar, in general that of *Macrotrichomonas unguis* is larger than that of *M. pulchra*, its middle part is broader, and the undulations are deeper and more numerous. The characteristic that most sharply differentiates this species from others, and from which the specific name is derived, is the presence of the unguis, a rectangular, shelflike, concave extension on the anteromedial edge just anterior to the angle at the origin of the posteromedial edge (pl. 17, figs. 31, 32). At its origin it is 4 to 4.5μ long, and it extends outward sharply for a distance of about 2μ. Its outermost edge is often ragged, and exceptionally it extends in a much longer, more irregular form. When the cresta, or at least its anterior part, is observed in a flat plane, and is to the observer's right in relation to the nucleus, the unguis extends upward in a more or less vertical direction. It stains more deeply with iron-haematoxylin than does any other part of the cresta; so that, when the cresta lies in the above-described position, and the unguis does not reach left of the anteromedial edge, it appears at first glance as an elongated thickening (pl. 17, fig. 34). The rest of the cresta may be decolorized when the unguis appears quick black, and then the unguis stands out very sharply. The structure occurs in all specimens of *M. unguis*, and it varies only moderately in size and shape. There is nothing like it in any specimen of *M. pulchra*.

In type and distribution the adherent spirochaetes are like those on *Macrotrichomonas pulchra*.

### **Macrotrichomonas ramosa** sp. nov.

(Pl. 18, figs. 35–45; pl. 19, figs. 46–48)

*Type host.*—*Glyptotermes brevicaudatus* (Haviland). Java.

T-4533. Bandjar. (Syntype slides TP-3217:19, 2.)

T-4540. Bandjar. (Homosyntype slides TP-3210:2, 6.)

*Diagnosis.*—Length 53 (36–64)μ; width 27 (20–40)μ; identical with *M. pulchra* in all characteristics except the parabasal body; parabasal turns 2½–7; one, two, or three rami of the parabasal present in most specimens, arising near the beginning of the coiled part, and either extending free, curved forward, or coiled with the main part of the parabasal.

The cresta has no semblance of the shelflike extension at the inner angle that characterizes *Macrotrichomonas unguis,* and in its size and form it is of the *pulchra* type. The trailing flagellum has a maximum width of about 2.5μ. Three anterior flagella were seen in many specimens. The rod at the base of the smaller root was not observed so distinctly as in *M. pulchra*, but there is some indication of it; no filament extends from this root to the angle of the nuclear rhizoplast, as occurs in *M. unguis.* No rodlets were present on the capitulum of the axostyle in the specimens studied. The bent nuclear rhizoplast, suspensorial lamella, and nucleus are exactly like those of *M. pulchra.*

The parabasal body also resembles that of *Macrotrichomonas pulchra* in the shape of the anterior part, the form, position, and attachment of the parabasal thread, and the number and form of the turns of the spiral. The presence of one or more branches or rami, however, readily distinguishes the species. These rami can be seen very clearly when Delafield stain is used, and that technique is distinctly advantageous in identification of the species. The presence of a ramus on the parabasal apparatus of *M. pulchra* is exceptional; only in a few individual specimens of hundreds examined has it been observed (Kirby, 1938*a*). The unusual occurrence in *M. pulchra* has developed into the usual condition in *M. ramosa.*

In the greater number of parabasals there is a single ramus, of variable length and direction, which generally originates from the first part of the spiral, just posterior to the nucleus (pl. 18, fig. 37). It ranges from a mere knob (pl. 18, fig. 38) to a cord of a length equal to that of the remaining part of the parabasal body beyond its point of origin (pl. 18, fig. 44). The ramus often extends forward, alongside of the nucleus, or free into the cytoplasm elsewhere. Sometimes it spirals with the main parabasal (pl. 18, fig. 45), and the apparatus is thus a double spiral for at least part of its length. Not infrequently there are two rami (pl. 18, fig. 40), and sometimes there are three (pl. 18, fig. 41), all originating in the same part of the parabasal. They may all be free; or one or two are coiled in the spiral. A ramus is seldom itself branched; this was observed in only one specimen (pl. 18, fig. 42).

On slides from T-4533 almost all specimens had at least one ramus. In a count of 100 there were 66 with one, 32 with two, and only 1 each with three and none. On several slides from T-4540 parabasals with no ramus were more frequent. In a count of 250 there were 116 with none, 111 with one, 21 with two, and 2 with three. Even in this series of preparations, however, more than half the specimens had a ramus, which is a very different situation from that in *Macrotrichomonas pulchra.*

In division stages in which there are two new parabasal bodies, these usually are unbranched, but several have been seen in which one of the two already had a ramus. In one double individual with two completely reorganized mastigonts each of the spiraled parabasals had a ramus of corresponding size and position.

Occasionally the anterior end of the parabasal is prolonged into a posteriorly directed extension of considerable length beyond the point that is closest to the blepharoplast, in the manner that is typical of *Parajoenia grassii* and certain other devescovinids. Usually, however, there is only a moderate enlargement at the anterior end.

In some Schaudinn-Delafield material heterogeneity is apparent in the structure of the parabasal throughout its length. There is deeply stained substance and unstained substance, arranged in rather constant relationship in two main types. Most often the structure suggests a series of arms on either side of a central column (pl. 19, fig. 48). These may be opposite, or not. The arms extend to the periphery, and between them are clear areas. Sometimes the appearance is that of two rows of vacuoles (pl. 19, fig. 47). In the second type the parabasal appears cross-banded, like striated muscle, the stained disks and clear intervening disks both reaching to the periphery (pl. 19, fig. 46). The different appearances are not correlated with any particular view of the parabasal body, or with any state of development. Both may be seen in different parts of the same parabasal, or in corresponding parts of different parabasals. Both types occur in rami as well as in the main structure.

In material stained with iron-haematoxylin there is the usual deep-staining filament at one edge of a less stainable homogeneous-appearing body (pl. 18, fig. 35).

### **Macrotrichomonas restis** sp. nov.

(Pl. 19, figs. 49–51; pl. 20, figs. 52–54)

*Type host.*—*Kalotermes jouteli* Banks. Florida.
T-4614. Englewood. (Syntype slides TP-3294:11, 12, 15.)
T-4616. Key Large. (Homosyntype slide TP-3296:11.)
*Other hosts*
? *Kalotermes jouteli* Banks. Mexico.
T-315. (Cleveland.) (Homosyntype slide TP-322:2.)
T-337. Socorro Island. (Homosyntype slide TP-290:1.)

*Diagnosis.*—(From type host): length 52 (41–65)μ; width 22 (17–28)μ; trailing flagellum a moderate cord, about the length of the body; cresta length 43 (37–52)μ, anteromedial edge 13 (11–15)μ, posteromedial edge 29 (23–34)μ; turns of parabasal spiral 3 (2¼–4), beginning several microns posterior to nucleus; capitulum of axostyle extended in an arm arising anteriorly, passing posteriorly and turned around trunk of axostyle, ending in a moderate membranous extension between the first turns of the parabasal; trunk of axostyle projecting, with no preceding enlargement, often 13–21μ; nucleus 7 (6–8.7) by 4 (3.3–4.7)μ; no adherent microörganisms. (From T-315): length 65 (49–87)μ; width 34 (21–49)μ; cresta length 33–49μ, anteromedial edge 8–11μ, posteromedial edge 20–31μ, maximum width 9–13μ; axostyle projecting 22 (15–27)μ; nucleus 6.3–10.7 by 4.6–6.2μ; no adherent microorganisms.

The material from Florida was determined by Professor A. E. Emerson, and that from Key Large was sent by Professor E. Morton Miller. A few slides of a termite labeled *Kalotermes jouteli* and recorded as from Mexico were sent by L. R. Cleveland; no specimens of this termite were preserved. Its faunule, however, corresponds to that of *K. jouteli,* and the original determination is probably correct. The one smear bearing this species from Socorro Island, Mexico, was made by Dr. A. E. Larsen from a collection of termites obtained in the interior of the island at an elevation of 1000 feet. The termites preserved from this collection were two alates, determined by Light (1935) as *K. marginipennis* (Latreille). The flagellates on the smear, however, are entirely different from those of *K. marginipennis* collected by Light at Tepic, Mexico, but agree with those of *K. jouteli* from Florida. It is possible that the smear from Socorro Island was actually made from a nymph of *K. jouteli* included in the collection with *K. marginipennis*. In a collection of *K. hubbardi*, made elsewhere at Socorro Island on the same day, Light found a soldier of *K. jouteli*. A few smears bearing flagellates of *Zoötermopsis* and *Cryptotermes* (?) were present in a series otherwise from *K. hubbardi*, indicating that mixture had occurred in the preparations from Socorro Island.

The trailing flagellum (pl. 19, figs. 49, 50) is a cord, not very stout, which follows the external edge of the long cresta and extends free beyond its end for a limited distance. It is actually distinctly separated from the cresta in fixed material, though in direction more or less paralleling it.

The inner angle of the cresta, at which the anteromedial edge meets the posteromedial edge, is always a few microns (often 4–6) posterior to the nucleus (pl. 19, fig. 51). In certain stained material the inner margin of the cresta along the posteromedial edge appears very different from the rest. It is differentiated as a thickened rib, which is broadest (often about 3$\mu$) at the angle and tapers gradually to the posterior end (pl. 19, fig. 51). It is stained deeply with haematoxylin in preparations in which the outer part of the cresta has retained scarcely any stain. The outer part is a thin membrane, and it requires a very heavy stain of the body to give it much color.

The nucleus of *Macrotrichomonas restis* is very close to the anterior end of the body (pl. 19, fig. 49). It is more elongated in shape than is customary in devescovinids. The elongation is in a longitudinal direction. The contents of the nucleus consist of a nucleolus and numerous small, deep-staining granules. The granules are rather uniform in size and are not very closely packed. They generally fill the interior, but sometimes a peripheral space exists. The chromatin mass often is pointed sharply posteriorly (pl. 19, fig. 49).

The parabasal body is often bent around the anterior end of the nucleus in a hook (pl. 20, fig. 54). The longitudinal part, which extends along the anteromedial edge of the cresta, is often about the same thickness as the rest; sometimes it is more slender or is flattened. The longitudinal part of the parabasal extends posteriorly to or beyond the angle of the cresta. The parabasal then passes obliquely to continue in the coiled part, the beginning of which is posterior to the nucleus by about the length of the nucleus (pl. 20, fig. 54).

A band-shaped chromophile element is present at the inner edge of the spiral (pl. 20, fig. 54). It continues along the longitudinal part, becoming slender, and has not been observed to separate from this. In its anterior part the main substance of the parabasal comes almost in contact with the blepharoplast, so there is no need for the filament to separate until it almost reaches the point of its junction with the granule.

The axostyle does not meet the posterior end of the nucleus, as is usual in devescovinids, but passes forward, on the left side, with limited expansion into the capitulum (pl. 20, fig. 52).

Particularly noteworthy is an arm that arises on the ventral side in the anterior part of the capitulum (pl. 19, fig. 51; pl. 20, fig. 52). This arm is of moderate thickness and is circular in cross section. It extends posteriorly, partly on the right side of the nucleus; and posterior to the nucleus it is turned around the trunk of the axostyle, approximately paralleling the first part of the parabasal. It terminates after continuing with the parabasal around the first turn of the tight spiral. At the end there is a membranous extension which could not be clearly interpreted, but its structure differs markedly from that to be described below in *Macrotrichomonas virgosa.*

Studies have been made of living specimens of *Macrotrichomonas restis* from termites sent from Florida. The observations were made on material diluted with 0.6-per cent NaCl solution. There was considerable activity of the body, but progressive movements were much restricted.

Movements of the papilla, accompanied by lashing of the whip of anterior flagella, took place continually. Sometimes, with the specimens confined as they were, there was a shifting of mastigont structures in the cytoplasm. The axostyle, parabasal body, and nucleus moved as a unit, the relative position of these parts undergoing no alteration. The axostyle, however, is somewhat flexible and the trunk in the cytoplasm bends.

The trailing flagellum undulates vigorously. For a time after the flagellates are removed from the host the movements are too rapid to be analyzed. The flagellum is applied to the surface of the body, above the edge of the cresta. It was not observed to separate even in moribund material, except when the flagellate actually disintegrated. In a specimen in which the cytosome burst, the flagellum separated from the surface before complete disintegration took place, and for a short time its undulations continued. On another occasion, movements of the trailing flagellum were observed when the flagellum was separated from the edge of the cresta. When specimens were killed by adding 2-per cent osmic acid, the flagellum did not separate; but when Schaudinn's fluid was added, many specimens showed the same separation that has been noted in permanent preparations. Even more marked separation occurred on killing in alcohol.

The outer part of the cresta is undulatory, and its movements cause a vibratory disturbance in the surrounding cytoplasm. They typically produce a cyclosis of cytoplasm in the peripheral zone, which appears to be particularly fluid. The current flows posteriorly on the crestal side and anteriorly on the opposite side, crossing over in the region of the capitulum of the axostyle. The more active the cresta, the more rapid the cyclosis. Not infrequently, in specimens under these abnormal conditions, the cresta shifts from one side of the cytosome to the other. The direction of cyclosis is then abruptly reversed.

This shifting of the cresta from one side to the other is a phase of the rotation of the whole mastigont structure, without alteration of the position of the main mass of the cytosome. Rotation was to the left, and occurred in jerks. Turning takes place and the cresta straightens out and undulates on one side; then another half-turn brings the cresta to the opposite side. In the intervals of shifting positions the cresta stops its undulations momentarily, bends, and straightens out again. The trailing flagellum is carried around with the cresta, but the surrounding cytoplasm changes. This behavior complicates the effort to understand the relationship of the trailing flagellum, the outer edge of the cresta, and the surface layer of the body.

Interior to the fluid peripheral zone the cytoplasm is of firmer consistency. In it most of the ingested particles are gathered, and, at least within a short period of time, they retain a constant relative position.

Around the trunk of the axostyle, just before it projects from the body, there is often present an aggregate of granules of variable size. Sometimes the aggregate is rather large. When this part of the axostyle shifts its position in the cytosome—as it sometimes does, so that it no longer projects through the same part of the surface membrane—the aggregate goes with it. This group of granules is firmly united to the trunk of the axostyle; and that fact is the more notable because the aggregate lies at the posterior end in the fluid peripheral zone, but moves not at all in cyclosis.

Lugol's solution did not stain the trunk of the axostyle or any elements in it.

## **Macrotrichomonas virgosa** sp. nov.

( Pl. 20, figs. 55–58; pl. 21, figs. 59–66)

*Type host.*—*Procryptotermes* sp. nov. Madagascar.
T-4359. Mahabo. (Syntype slides TP-3134:5, 6.)
T-4307. Near Maevetanana. (Homosyntype slide TP-3094:17.)
T-4400. Ankazoabo. (Homosyntype slide TP-3149:13.)

*Diagnosis.*—Length 43 (26–61)μ, width 19 (9.5–36)μ; distance from anterior end to nucleus as in *M. pulchra;* trailing flagellum a moderately stout cord, equal to or somewhat longer than the body; cresta length 22–45μ, anteromedial edge 5–8μ, breadth in middle about 4–8μ, stout, deep-staining rib along posteromedial edge; turns of parabasal spiral usually 2½–4, range 1–6, beginning immediately posterior to nucleus; chromatic shield constantly present along the left side of the nucleus, reaching to within a few microns of the posterior end of the nucleus; capitulum of axostyle with arm arising anteriorly, passing posteriad, terminating in a troughlike membrane within the first turn of the parabasal; trunk of axostyle tapered evenly, with no enlargement at point of projection, projecting from the posterior end often 18 (8–28)μ; nucleus elongated longitudinally, 5.5–10 by 2–4.5μ, no pointed extension along trunk of axostyle; rods often 2.5–7μ long adherent to the posterior part of the body, with a cuplike structure in the cytoplasm at the point where each adheres; spirochaetes often 20–30μ, ranging up to 50μ, adherent to the posterior or other parts of the body of most specimens.

The more anterior of the two roots that pass along the papilla is the stouter. At the proximal end of each root is an enlargement, that of the posterior root being a more definite granule. These two ends are each connected by a slender filament to a granule a short distance away, which apparently is the one that is joined by the cresta. Close to it is a granule that is met by the trailing flagellum.

In the papilla, along the roots of the anterior flagella, are often two or three uneven rows of granules or short rods (pl. 20, fig. 55). They extend from the blepharoplast a variable distance toward the tip of the papilla. In many specimens there are few or none of these papillar granules.

The chromatic shield is separated by only a short distance from the cresta on the left side of the nucleus. It extends from the region of the blepharoplast to about the level of the posterior end of the anteromedial edge of the cresta. The granules of the chromatic shield are for the most part considerably smaller than the papillar granules. The chromatic shield is constant in occurrence, position, and form.

The anteromedial edge of the cresta is applied to, or situated very close to, the nuclear membrane (pl. 20, fig. 55). Its junction with the posteromedial edge is anterior to the posterior end of the nucleus; in this there is a difference from *Macrotrichomonas restis,* in which the angle is always posterior to the nucleus at a not inconsiderable distance (pl. 19, fig. 51). For more than half its length the cresta has a width that is about equal to the length of the anteromedial edge. The inner margin of the cresta, as in *Macrotrichomonas restis,* is a sharply defined rib that tapers from a width of 2–4$\mu$ to a stout filament (pl. 20, figs. 55, 56). It is thickened, whereas the remainder of the cresta is a thin membrane. For two-thirds or so of its width this membrane is flat and stains with iron-haematoxylin to a deeper tone than does the outer third. The outer part is clear and deeply undulated. Its margin is typically at the edge of the body, but often it projects or extends that edge outward.

In many specimens the cresta extends more or less longitudinally for its full length, or obliquely with a certain amount of spiraling. In some flagellates the cresta, extending longitudinally for about half its length, turns abruptly transversely or even anteriad, so that its posterior end is near the anterior end of the body. Sometimes the whole cresta is curved more and more closely, in an increasingly transverse axis, until it forms a circle around the nucleus. It is not known how closely these positions of the cresta in fixed material accord in this species with the situation in living material.

The trailing flagellum (pl. 20, fig. 55) is a cord like that of *Macrotrichomonas restis.* In many specimens on the slides examined it follows the edge of the cresta, but there is a very narrow clear space between it and that edge. In many other specimens it is separated more or less. The flagellum becomes more slender where it continues free beyond the posterior end of the cresta.

The parabasal body passes anteriorly along the nuclear membrane, following it closely to the anterior end. Here its substance is extended forward in a bluntly pointed conical structure (pl. 20, fig. 58; pl. 21, figs. 59, 60). This cone is sometimes attached to the rest of the parabasal by a narrowed region, or is even entirely separated from it. Breaks along the substance of the parabasal occur in occasional specimens (pl. 21, figs. 59, 61). In a few specimens a short or long ramus arising in the anterior part of the spiral has been observed (pl. 20, fig. 58; pl. 21, fig. 63).

The first turn in the parabasal spiral surrounds the axostyle just posterior to the nucleus (pl. 20, fig. 55); in this there is a marked distinction from *Macrotrichomonas restis* (pl. 20, fig. 54). The first loop is typically a good deal wider than the following ones, which turn very closely around the axostyle. There is a certain distance between the successive turns; this space is broad between the first and second turns.

The trunk of the axostyle approaches the posterior end of the nucleus in more nearly the customary manner than does that of *Macrotrichomonas restis.*

A moderately expanded capitulum continues forward on one side of the nucleus. Arising in the anterior part of the capitulum and extending posteriorly is an arm (pl. 20, fig. 56) like the capitular arm of *M. restis*. Its proximal part is ventral to the nucleus. It then extends obliquely dorsad toward the inner angle of the cresta, passing on the left side of the nucleus. When it nears the cresta it loses its form of a cylindrical arm, and becomes a trough-shaped membrane. This membrane winds around the trunk of the axostyle, inside the first turn of the parabasal body. The bottom of the trough lies close to the trunk of the axostyle, but its sides are widely flared. One side of the membrane can be followed forward along the ventral edge of the main part of the capitulum, so it seems to have a double origin. No such elaborately developed membrane has been seen at the end of the capitular arm of *M. restis*. This probably is not merely a matter of the structures revealed by differing technique. The material studied has been of comparable quality, and there seems to be a definitely less elaborate development in *M. restis*.

The nucleus is elongated longitudinally, broadly rounded posteriorly, and narrowed anteriorly. Small granules form a mass that fills the space enclosed by the membrane almost or quite completely. The nucleolar substance is in one or two relatively small spherules. There is no posterior point or conical extension.

Rod-shaped microörganisms are adherent to the posterior part of the body of practically all specimens. The number present varies considerably, from a few around the projecting axostyle to many reaching more than halfway toward the anterior end.

There are two types of them. One type consists of straight or slightly curved rods with rounded ends and very little or no tapering. Most of these have a length of 2.5–7$\mu$, and a width of about $\frac{1}{4}$–$\frac{1}{2}\mu$. A number of deep-staining granules of relatively large size are present in their cytoplasm. Stages in transverse division occur. The rods of the other type are stouter, deeper-staining, and have tapered ends. Many of them are 4–9$\mu$ in length. Stages of transverse division are numerous. Though there is a notable difference between typical forms, the two types intergrade.

Much larger rods, often about 25$\mu$ long, similar in form to those with rounded ends, and with scattered deep-staining granules in the cytoplasm, are abundant in the gut contents of the termite. They have not been observed adhering to the flagellates. There are also smaller forms of this free rod, leading to intergradation in size with the attached ones. It seems most likely that the two are separate organisms, but there is no proof of this conjecture.

Where each of the rods with rounded ends meets the body, there is a deep-staining cup-shaped structure (pl. 21, figs. 64–66). This is embedded beneath the surface, and appears to be a structure of the cytoplasm. The edges of the cup often extend a little beyond the edges of the rod, and the size relationship is to the size at the end. Smaller rods have smaller cups, and in those with tapered ends the intracytoplasmic body is narrow and shallow, often more a granule than a cup. The region of the cytoplasm adjacent to the cup is clearer than the rest.

Evidence that the cup is a cytoplasmic structure is afforded by the frequent detachment of the rods. This occurs often on the smears, the rods then usually being present in the right direction toward the body but a short distance away (pl. 21, fig. 64). Detachment is probably caused by the operation of smearing, but evidently is unusually easy. The cup remains in position in the cytoplasm.

The cups have been seen most clearly in Hollande-fixed material, but they are evident also in iron-haematoxylin-stained material after other fixatives.

The other adherent microörganisms, long spirochaetes, are less constant in occurrence than the rods. They are usually, but not always, restricted to the posterior end; and many specimens lack them.

### **Macrotrichomonas lighti** (Connell) comb. nov.

(Pl. 22, figs. 68–72)

*Gigantomonas lighti* Connell, 1932, Univ. Calif. Publ. Zoöl., 37:156, pls. 8, 9, figs. 1–15, text figs. A–C.

*Type host.—Paraneotermes simplicicornis* (Banks). California, Arizona.

T-355. Southern California. (Xenosyntype slides TP-326:7, 8, 9, from original material used by Connell.)

*Diagnosis.*—Length 68 (47–91)μ (Connell), 68 (52–90)μ (original), width 38 (21–58)μ (Connell), 38 (24–49)μ (original); trailing flagellum a band, about 1.5 (1.2–1.7)μ, one edge deeper-staining than the rest; average measurements of cresta (Connell), length about 70μ, anteromedial edge about 23μ, posteromedial edge about 50μ; measurements of cresta (original), length 68 (49–86)μ, anteromedial edge 25 (15–31)μ, posteromedial edge 41 (28–47)μ; riblike thickenings reinforcing medial edges of cresta, each with a bulbous enlargement at the angle between the medial edges, external margin sculptured by short, slender lines perpendicular to edge; cresta vigorously undulatory; parabasal spiral beginning posterior to nucleus, a distance usually equaling or exceeding the nuclear diameter, turns 6–12 (Connell), 8 (6–9+) (original); nucleus pyriform or top-shaped, pointed posteriorly, 10–12 by 5.5–7.8μ (Connell), 9.8 (8–12) by 7.2 (6–9.3)μ (original); no regularly adherent microörganisms.

The papilla, along the anterior edge of which the bases of the three anterior flagella adhere, is relatively small. At the base of the papilla, close to the anterior end, are two granules, one posterior to the other, about equal in size, and interconnected by a very well-defined, somewhat curved fibril (pl. 22, fig. 68). To the anterior of these granules Connell applied the term blepharoplast; to the posterior, centriole. He apparently established the fact that the latter divides, and around the fibril connecting the resulting two the paradesmose develops.

The anterior flagella, according to Connell, are about 40μ long, and the longer trailing flagellum surpasses the length of the body. The anterior flagella have two roots: one stouter than the other, and ending in a clublike enlargement connected by a fine fibril to the blepharoplast; the second, finer, and passing directly to the blepharoplast. One border of the band-formed trailing flagellum (pl. 22, fig. 69) stains more deeply than the rest of its substance. Connell used the term marginal flagellum for this border, and referred to the whole band-shaped structure as the undulating membrane. This, I believe, is incorrect; the band as a whole is the trailing flagellum, as is that of *Devescovina lemniscata.*

Connell stated that in *Macrotrichomonas* the "base of the undulating membrane" (trailing flagellum) is fused to the margin of the cresta. I do not agree that this is actual fusion. The trailing flagellum commonly follows the margin of the cresta, and appears to be adherent to the body surface there (pl. 22, figs. 70, 71), as is true in other devescovinids. But no attachment is apparent in some fixed material, and the separation cannot be explained as being due solely to abnormal tearing "by careless smearing and bulk fixation." Certainly, this easy separation indicates no fusion of an undulating membrane, like that in *Trichomonas,* to the surface of the body.

For a description of the cresta the reader is referred to Connell's accurate account. The thick reinforcements along the anteromedial and posteromedial edges (pl. 22, figs. 70, 71) represent an advance in development over other known species of *Macrotrichomonas.* The sculpturing of the external margin by close, short, perpendicular lines (pl. 22, fig. 72) also is a unique feature of this species. I cannot subscribe to Connell's statement that the "anteromedial edge is firmly fused to the axostyle." The point cannot be decided from observation of this species alone, but comparison with other devescovinids makes it improbable that there is an actual fusion. The relative position of this edge to the axostyle, however, remains constant except in dividing specimens.

The cresta does not stain well with iron-haematoxylin; although that stain, after Schaudinn fixation, in most other devescovinids which I have studied blackens the whole structure, and is not readily extracted. In *Macrotrichomonas lighti,* after fixation in Schaudinn's, Zirkle's, or Champy's fluids, or osmic vapor, iron-haematoxylin stains the outer edges and the sculpturing as black lines, and blackens the ribs, but the inner parts of the cresta remain colorless even in heavily stained material.

The cresta undergoes vigorous intracytoplasmic undulatory movements. Connell observed this activity in living material, and I have watched it in many specimens.

The trunk of the axostyle is stout, and its short, projecting end is tapered to a point. It is composed of a core and a surrounding sheath. According to Connell, the sheath is composed of many delicate fibrils, so that the axostyle has a striated appearance. However, I have observed no evidence that the sheath is fibrillar. The internal differentiation of a core within the sheath sometimes gives a superficial appearance of a fibrillar structure, but this appears only at a focus deeper than the sheath. It seems certain that the sheath is a continuous membrane, as in other devesecovinids.

Connell gave the diameter of the axostyle immediately posterior to the nucleus as 8μ, and at the posterior end of the body as 5μ. According to my measurements, however, near the nucleus the axostyle is about 5μ broad, at the beginning of the parabasal coils about 3μ, and at the posterior end of the body about 1.5μ.

Connell described as constant in occurrence a chromatic shield consisting of a shield-shaped aggregation of chromatic granules lying against the capitulum of the axostyle. In my material such granules were present in *Macro-*

*trichomonas lighti* as in many other devescovinids, but they were not usually arranged in so constant and definitely formed an aggregation. This fact, however, does not invalidate Connell's account of the chromatic shield, which I have observed in many devescovinids.

The parabasal body is a long, cylindrical structure of approximately equal diameter throughout its length (pl. 22, fig. 69). Its posterior portion is wound in a tight, close spiral around the trunk of the axostyle in from 6 to 12 turns, usually 6–8. The close spiral begins at a distance often equaling or exceeding the nuclear diameter posterior to the nucleus, instead of just posterior to this, as in most devescovinids. The anterior part passes along the nuclear membrane, but instead of ending on the anterior surface of the nucleus, as is usual in *Devescovina,* it continues anteriorly toward the blepharoplasts.

Connell stated that the parabasal body is joined to both the anterior granules, a filament along its anterior margin meeting the one he termed the blepharoplast, and one along its posterior margin meeting the one he termed the centriole. The centriole is, he stated, embedded in a matrix of less stainable substance which lies just posterior to the blepharoplast and is elongated in a transverse direction; and the substance of the parabasal body meets one side of this centrosome matrix. But the two do not, in Connell's text figure, coincide altogether, for the parabasal meets the blepharoplast and the matrix does not extend so far anteriorly as this.

My interpretation of the anterior end of the parabasal body (pl. 22, fig. 68) is one that accords more exactly with the structure usual in devescovinids. The so-called centrosome matrix is the anterior end of the parabasal body itself. This is very clear in Zirkle–iron-haematoxylin, and in Schaudinn-Delafield material. The granule ("centriole") is not embedded in the parabasal, but lies against its surface, a short distance from its end. A filament extending along the edge of the parabasal, the parabasal filament, meets this granule. The parabasal substance is extended a little beyond the granule at the end of the filament. The line that Connell thought to be an attachment of the parabasal to the anterior granule (blepharoplast) is the inner border of the cresta.

With this interpretation of the anterior structures, a closer similarity in them is found to exist between *Macrotrichomonas lighti* and *M. pulchra* than is apparent from Connell's account. In both there are two roots of the anterior flagella, one stouter than the other, and these attach to the blepharoplast in the same way. To this granule the cresta and trailing flagellum also attach. The granule posterior to this, which Connell considered to be the centriole, may be homologous with the larger posterior granule of *M. pulchra.* The parabasal filament attaches to one side of this and the nuclear rhizoplast to the other, in a manner similar to that in which the homologous filaments of *M. pulchra* meet the posterior granule. There is, of course, difference in detail. The larger granule of *M. pulchra* is replaced by a filament and small granule, and the latter lies against the parabasal body.

The conspicuous filament termed by Connell the suspensory filament is not homologous with the suspensorial lamella of *Devescovina hawaiensis* and *Macrotrichomonas pulchra,* but is the same as the nuclear rhizoplast of *M.*

*pulchra.* This leaves the so-called centriole, passes horizontally along the side of the parabasal and beyond, and then curves posteriorly to meet the nuclear membrane near the anterior end (pl. 22, fig. 68). It apparently runs along the surface of the nucleus for a short distance. I have been unable to verify the existence of the rhizoplast described by Connell as extending from the so-called centriole to the nuclear membrane. In the specimen drawn the various fibrils are very distinct, but there is no indication of this one. The lamella shown in figure 68 as passing from near the end of the papilla to the side of the nucleus appears to be homologous with the suspensorial lamella of *D. hawaiensis* and *M. pulchra.*

The behavior of moribund specimens of *Macrotrichomonas lighti* is of unusual interest. The behavior described below has been observed in a sufficient number of individuals to insure that it is of general occurrence in this species. It takes place in animals which have been for some time in 0.6-per cent sodium chloride solution between a slide and coverglass. After a period in which form and movement have apparently been normal, the body suddenly rounds up and all movement ceases. Activity begins again after a few minutes, and may become vigorous. The axostyle, which has become curved within the rounded body, is soon broken off sharply just posterior to the spiral of the parabasal. The cytoplasm becomes more fluid, indicated by increased Brownian movement of the granules. The nucleus, the remaining part of the axostyle, the parabasal, and the cresta remain intact, the last sinking more deeply into the body. These organelles are no longer anchored in one place, but move laterally in the cytoplasm or revolve, apparently propelled by undulations of the cresta.

The trailing flagellum behaves in a remarkable manner, which was the same in all of many instances observed. It becomes entirely enclosed in the cytoplasm, and its posterior part, within a surrounding vacuole, becomes crimped in the form of a ruffle. The crimping progresses anteriad, the vacuole moving forward, until all but a short anterior portion of the flagellum is enclosed in the vacuole in a ruffle form extending around the periphery. The vacuole is always situated in a similar region, beside the nucleus. Regular undulatory movements of the flagellum continue, so that the rufflelike contents appear to be constantly revolving in the vacuole. These rhythmic movements of the flagellum continue after all other movements of the flagellate have ceased.

### **Macrotrichomonas procera** sp. nov.

(Pl. 22, fig. 67)

*Type host.*—*Calcaritermes brevicollis* Banks. Panama.
T-197. Barro Colorado. (Syntype slides TP-113:2, 6, 9.)
*Additional hosts*
*Calcaritermes emarginicollis* Banks. Costa Rica.
T-171. Estrella. (Homosyntype slides TP-106:8, 17.)
*Calcaritermes nearcticus* Snyder. Florida.
T-531. Bartow. (E. M. Miller.) (Homosyntype slide TP-534:2.)
*Calcaritermes parvinotus* Light. Mexico.
T-265. (Light 183.) Colima. (Homosyntype slides TP-225:9, 10.)

*Diagnosis.*—(From type host): length 56 (42–65)μ; width 19 (16–24)μ; distance from anterior end to nucleus 18 (15–21)μ; trailing flagellum a narrow band staining uniformly;

**cresta length 45 (41–51)μ, anteromedial edge 27 (25–32)μ; posteromedial edge 17 (13–20)μ; paracrestal filament represented by a frequently broken band parallel to the anteromedial edge of cresta; longitudinal part of parabasal body unusually long, spiral part turned 1–4½, usually 1½–3, times; nucleus spheroidal or ellipsoidal, 7.3 (6.7–8) by 4.8 (4–6)μ; numerous adherent spirochaetes, especially on anterior and posterior portions. (From *Calcaritermes emarginicollis*): length 52 (38–61)μ; width 20 (14–26)μ; cresta length 41 (36–45)μ, anteromedial edge 27 (21–29)μ, posteromedial edge 14 (12–18)μ; nucleus 7.5 (6.7–9.3) by 5.3 (4–6.7)μ.**

An outstanding difference between *Macrotrichomonas procera* and other species of the genus is that in the former the nucleus is shifted posteriorly to a marked degree; and there is a corresponding elongation of the anterior portions of the cresta and parabasal body (pl. 22, fig. 69).

The anterior granules and attached organelles are arranged similarly to those in *M. pulchra.* The anterior flagella terminate in two roots one larger than the other and dividing into two flagella. The trailing flagellum ends in a separate small granule, and the cresta apparently also ends separately. A suspensorial lamella like that of *M. pulchra,* but longer, is present. Close to it may be seen the edge of the capitulum of the axostyle.

The trailing flagellum is about half the width of that of *Macrotrichomonas pulchra.* In general it follows the contour of the undulated crestal margin, but nevertheless may be at a considerable distance from it. It often departs from the parallelism in places and sometimes altogether, and it is clear that at least in Schaudinn-preserved material it is not fixed to the edge of the cresta.

The cresta extends for from half to three-quarters or more of the length of the body. The anteromedial edge is, unlike the condition in the other species, considerably longer than the posteromedial edge. The angle between these edges is located in a position a short distance posterior to the nucleus, corresponding to its position in most other species. The inner margin stains more deeply than the rest, but there are no sharply demarcated thickenings like the ribs of *Macrotrichomonas lighti.* Parallel and close to the anteromedial edge of the cresta is a structure evidently homologous with the paracrestal filament of *M. pulchra.* It is, however, less sharply defined, stouter, and deeper-staining than the anterior part of that structure in *M. pulchra.* Sometimes it appears as a continuous band, but more generally it is in part split or broken into granules. It ends near the nucleus, and does not have an enlarged posterior portion extending posterior to the crestal angle. Anteriorly it terminates separately from the cresta.

The parabasal body is of even thickness for its entire length, and the spiral is closely wound. The posterior end of the axostyle projects beyond the end of the body, often for a not inconsiderable distance; and it is tapered gradually to a point.

The nucleus is spheroidal, ellipsoidal, or irregular in outline. When there is an elongation, it is more often longitudinal than like that in the specimen figured. Sometimes the chromatin mass is pointed anteriorly, or irregularly angular, but it is not generally extended in a point posteriorly as is frequent in other species. The chromatin mass is granular, but the granules are not so coarse or deep-staining as in many other *Macrotrichomonas* nuclei.

There is usually a small tuft of moderately long spirochaetes on the papilla, and many spirochaetes are adherent to a considerable area of the posterior part of the body.

## SUMMARY

Descriptions are given of 6 species of *Caduceia,* of which 3, *C. bugnioni, C. monile,* and *C. kalshoveni,* are new. One name, *Caduceia pruvoti* (Duboscq and Grassé), is a new combination.

There is a close relationship between the genera *Caduceia* and *Devescovina.* The former genus is not common, having been found in 9 species of termites, whereas *Devescovina* has been recorded from more than 60.

The flagellates are relatively large in size, the trailing flagellum is relatively slender and short, and the parabasal body is relatively large and is turned in a spiral. Outgrowth of rami is characteristic of the parabasal of one species, *Caduceia nova.* In all species there is a dense investment of spirochaetes on all or most of the surface. *Fusiformis*-like rods are present on several.

The two species found in African termites, *Caduceia theobromae* and *C. nova,* are closely related to one another; as is true also of the two species found in Javan termites, *C. monile* and *C. kalshoveni.* The last two species named have in common, though with individual differences, an anteriorly located ring—a unique structure, not observed in other devescovinids.

Reasons are given for considering *Macrotrichomonas* Grassi to be a separate genus from *Gigantomonas* Dogiel. Descriptions are given of 7 species of *Macrotrichomonas,* of which 5, *M. unguis, M. ramosa, M. restis, M. virgosa,* and *M. procera,* are new. One name, *Macrotrichomonas lighti* (Connell) is a new combination.

In *Macrotrichomonas* there is a very large cresta, which at least in some species is undulatory. The trailing flagellum adherent to its external edge is a cord or band relatively longer than that of *Caduceia.* The parabasal body is large and spiraled; outgrowth of rami is characteristic of one species, occurs rarely in others. An unusual development of the capitulum of the axostyle, observed in several species, is an armlike structure arising in the papillar region and passing posteriad to near the beginning of the parabasal spiral. The trunk of the axostyle is not filamentous posteriorly within the cytoplasm, as is usual in *Devescovina* and *Caduceia;* and it generally projects from a very little to a considerable distance. An unusual feature in *M. procera* is the great elongation of the body anterior to the nucleus.

Activity of the living flagellates, in which there are undulatory movements of the cresta, with synchronized undulations of the trailing flagellum, and sometimes rotational movements of the mastigont structures in the cytosome, is described in *Macrotrichomonas restis.* Similar activity has been observed in *M. lighti.* In that species when moribund the axostyle has been observed to become broken off within the body; and the trailing flagellum, continuing to undulate, becomes enclosed and wound up in a vacuole near the nucleus.

Adherent spirochaetes are often present, and of special interest are the rods on *Macrotrichomonas virgosa.* These are larger in size than most rods adherent to other devescovinids, have a number of chromatic granules in their cytoplasm, and are insecurely adherent by an end to the surface of the flagellate. This end fits into the concavity of a deep-staining body in the cytoplasm of the flagellate, and detaches from that body under certain circumstances.

*Macrotrichomonas* is present in many termites of the genus *Glyptotermes;* most often the flagellate in them is *M. pulchra,* which is the species in more than half the termites in which *Macrotrichomonas* has been found. The flagellate genus is represented also in a number of other genera of Kalotermitidae.

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# PLATES

All figures have been drawn with the aid of the camera lucida.

Abbreviations for methods of preparation: B., Bouin's fluid; C., Champy's fluid; D., Delafield's haematoxylin; E., eosin; Er., erythrosin; F., acid fuchsin; Fl., Flemming's fluid; H., iron-haematoxylin; Holl., Hollande's fluid; Os.V., osmic vapor; R., Regaud's haematoxylin; S., Schaudinn's fluid.

## PLATE 10

Fig. 1. *Caduceia theobromae* França from *Kalotermes* (s.l.) sp. T-4240. Parabasal body with one short ramus; in the majority of specimens there is no branching. Spirochaetes on entire surface except the posterior area, where adherent rods are present. S.H. × 1335.

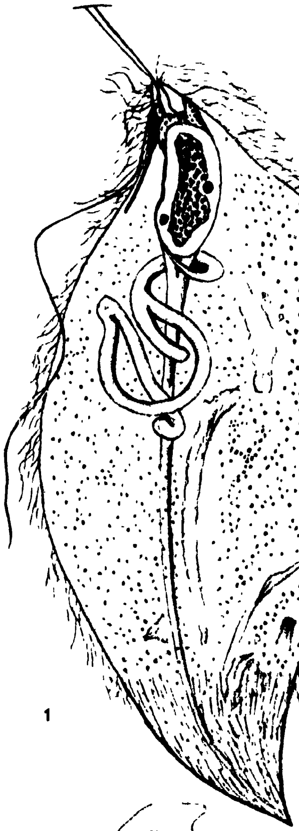
Figs. 2–4. *Caduceia nova* (Grassi) from *Neotermes* sp. T-2012.

Fig. 2. Entire; coat of spirochaetes; the area bearing adherent rods, which is not shown, is on one side of the body, so that spirochaetes occupy the posterior area; trunk of axostyle curved within cytoplasm; parabasal with 3 rami; S.H. × 1400.

Fig. 3. Parabasal with 5 rami, and a short secondary branch on one of these. F.R. × 1400.

Fig. 4. Parabasal body with 5 rami. F.R. × 1770.

Scale × 1400.



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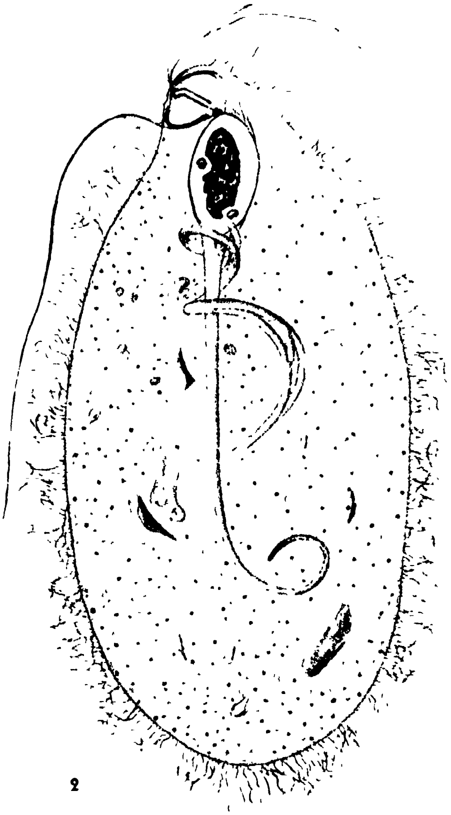

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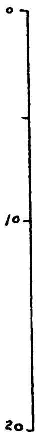

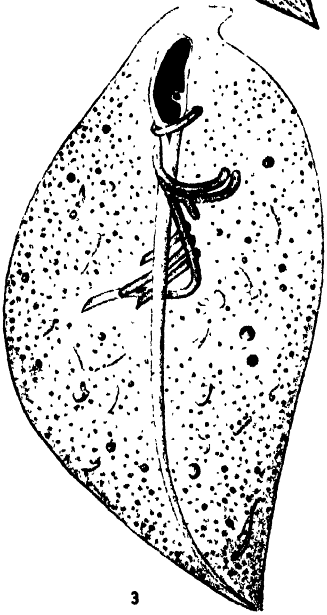

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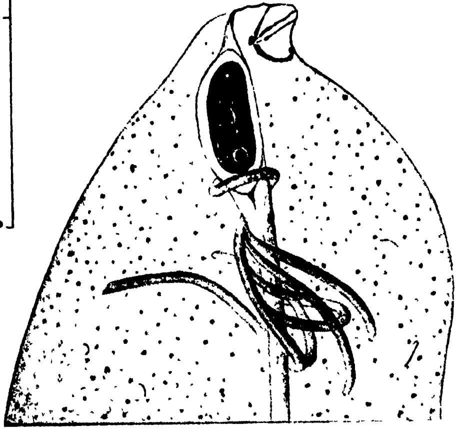

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# PLATE 11

**Fig. 5.** *Caduceia nova* (Grassi) from *Neotermes* sp. T-2012. Detail: blepharoplast group; origin of flagella; short rod extending from blepharoplast; cresta; anterior part of parabasal filament, bending close to the anteromedial edge of the cresta; chromatic shield on crestal side of nucleus; nuclear rhizoplast; first loop of parabasal body. S.H. × 2400.

Figs. 6–10. *Caduceia bugnioni* sp. nov. from *Neotermes greeni.*

**Fig. 6.** Entire: complete covering of spirochaetes shown, adherent rods omitted; axostyle completely enclosed in cytoplasm; full length of flagella; cresta minute; chromatic shield on crestal side of nucleus. S.H. × 1400.

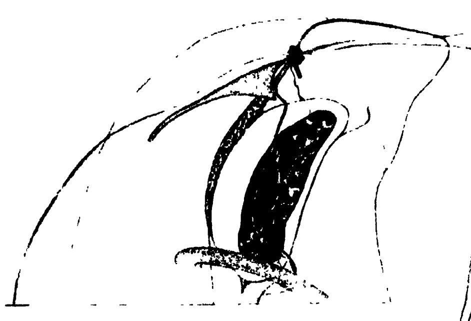
**Fig. 7.** *Fusiformis*-like rods arranged in transverse bands; spirochaetes shown at edge only. S.H. × 1400.

**Fig. 8.** Parabasal body; the Delafield-staining substance continues longitudinally in a slender anterior part; the parabasal filament separates from this, and bends outward toward the cresta with a sharp angle near the blepharoplast. S.D. × 2400.

**Fig. 9.** Flagellar roots with flagellar granule at end of one, blepharoplast at end of other; cresta and trailing flagellum; nuclear rhizoplast; anterior extension of capitulum of axostyle; parabasal filament a band in spiral part of parabasal, passing forward to blepharoplast with a sharp angle near the cresta. S.H. × 2400.

**Fig. 10.** Granules of chromatic shield observed partly above nucleus; the cresta has been displaced. S.H. × 2400.

Scale × 2400.



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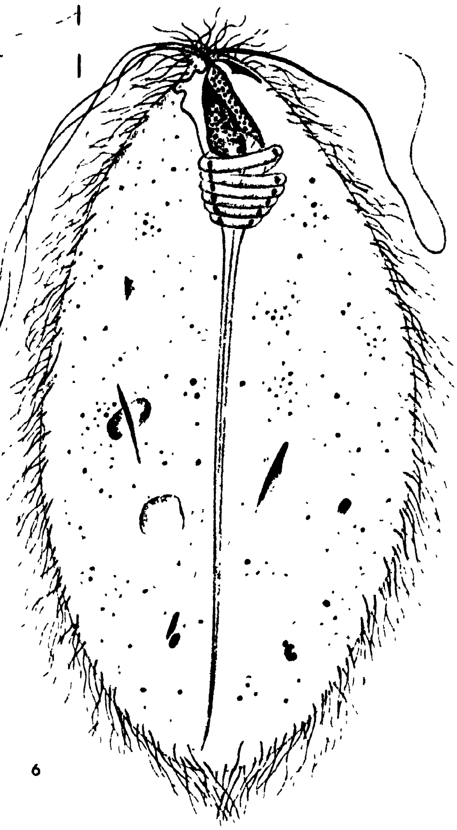

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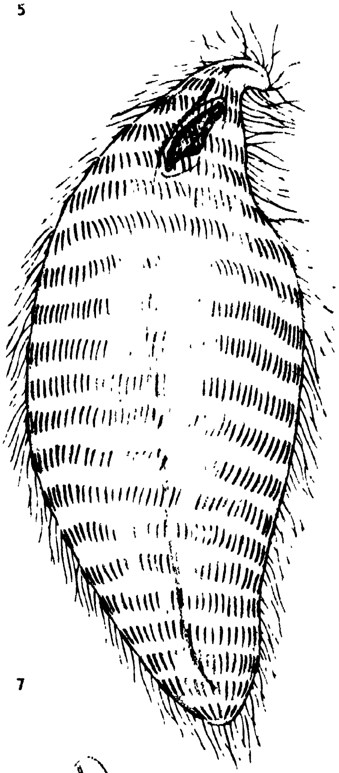

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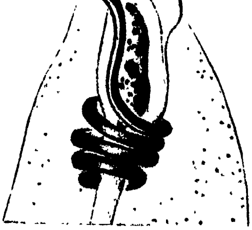

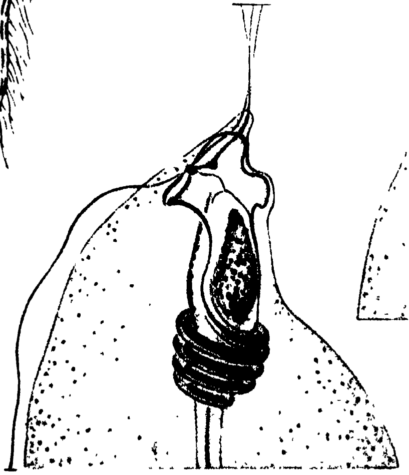

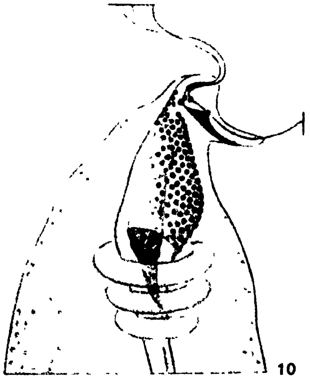

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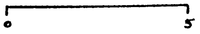


## PLATE 12

Figs. 11–13. *Caduceia bugnioni* sp. nov. from *Neotermes greeni.*

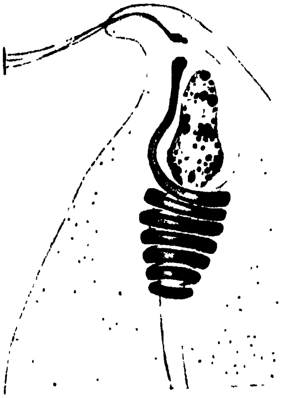
Fig. 11. Parabasal body. S.D. × 2400.

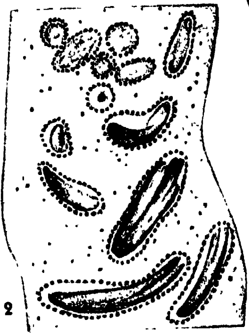
Fig. 12. Particles of wood in cytoplasm, showing surrounding vacuoles and small granules at edge of vacuole. S.H. × 1400.

Fig. 13. Anterior structures: capitulum of axostyle; chromatin mass of nucleus drawn to point anteriorly and posteriorly; parabasal thread shown in optical section at inner edge of spiral. S.H. × 2400.

Fig. 14. *Caduceia kalshoveni* sp. nov. from *Neotermes dalbergiae.* Entire: spirochaetes covering entire surface; anterior extension of capitulum of axostyle; minute cresta; flagellar granule and blepharoplast; trunk of axostyle tapering and completely enclosed in cytoplasm. S.H. × 1400.

Scale × 1400.





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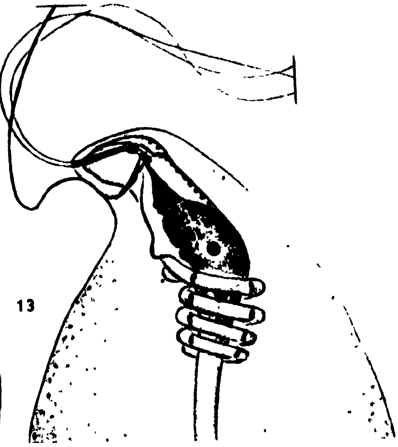

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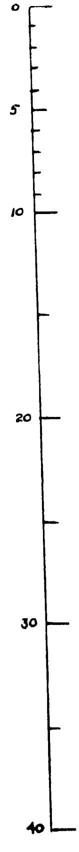

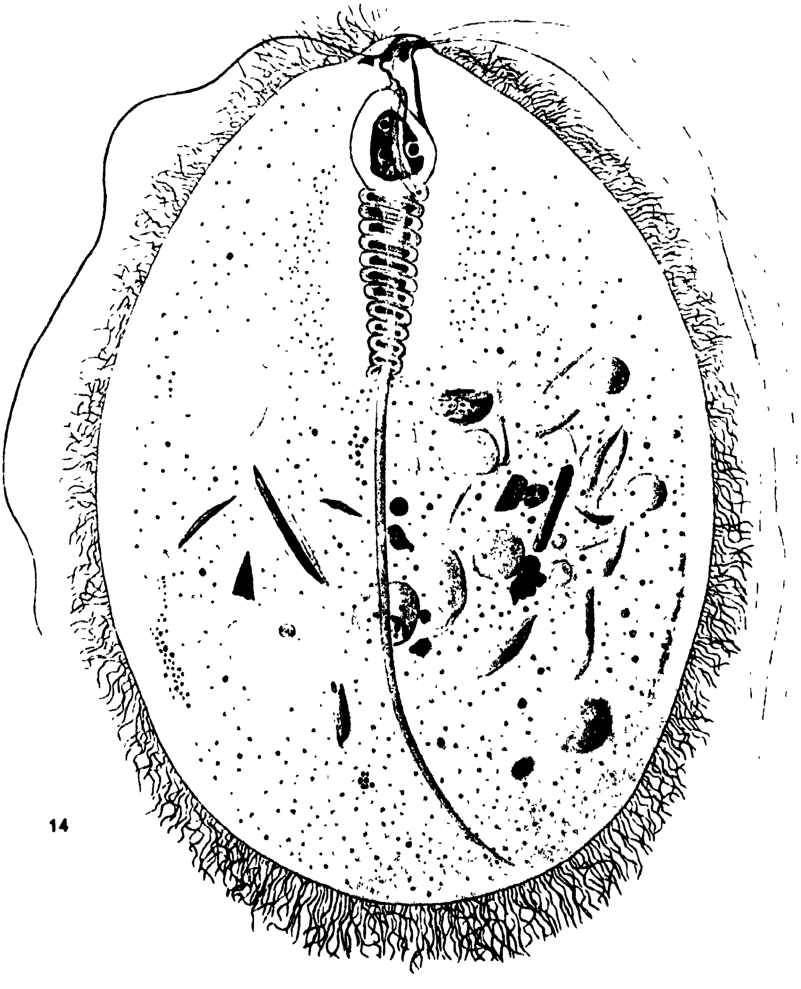

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## PLATE 13

Figs. 15–17. *Caduceia kalshoveni* sp. nov. from *Neotermes dalbergiae.*

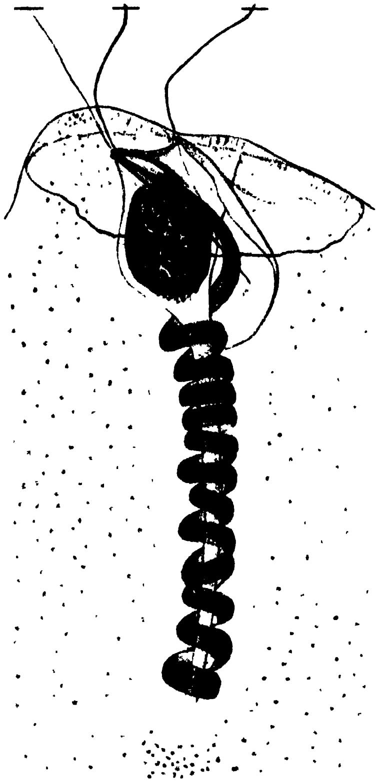
Fig. 15. Very early division stage; paradesmose short, two flagella at one pole, one at the other; old parabasal attached at one pole, intact and spiraled; new parabasal developing at other pole; ring intact. F.R. × 1770.

Fig. 16. Detail: origin of flagella from blepharoplast group and elongated flagellar granule; slender ring near base of papilla; the stout filaments anterior to the nucleus are optical edges of the capitulum. F.R. × 2400.

Fig. 17. Section: character of ectoplasm and endoplasm; transverse cut of parabasal spiral, showing parabasal filament on inner edge. S.H. × 1770.

Fig. 18. *Caduceia monile* sp. nov. from *Neotermes tectonae.* Entire, except for most of length of anterior flagella; stopper shape of papilla, with ring at base of anterior protuberance; spirochaetes covering body; rod-shaped bacteria aggregated in region of nucleus. S.H. × 1400.

Scale × 1400.



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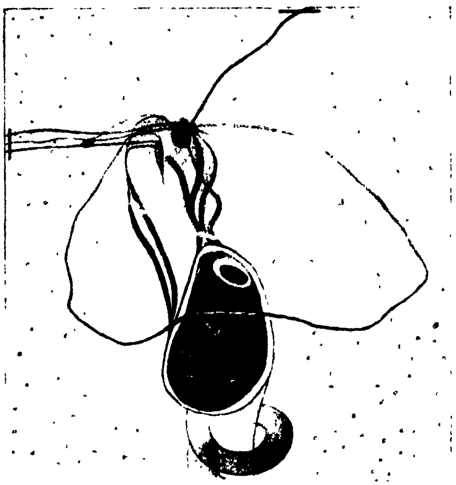

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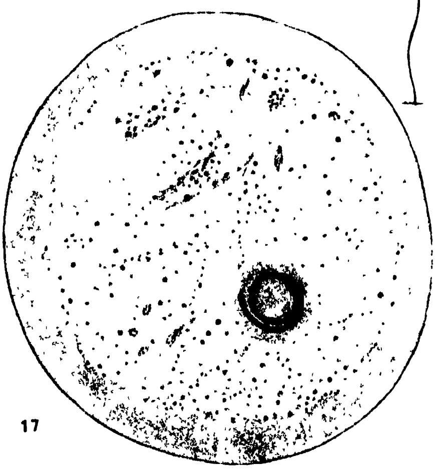

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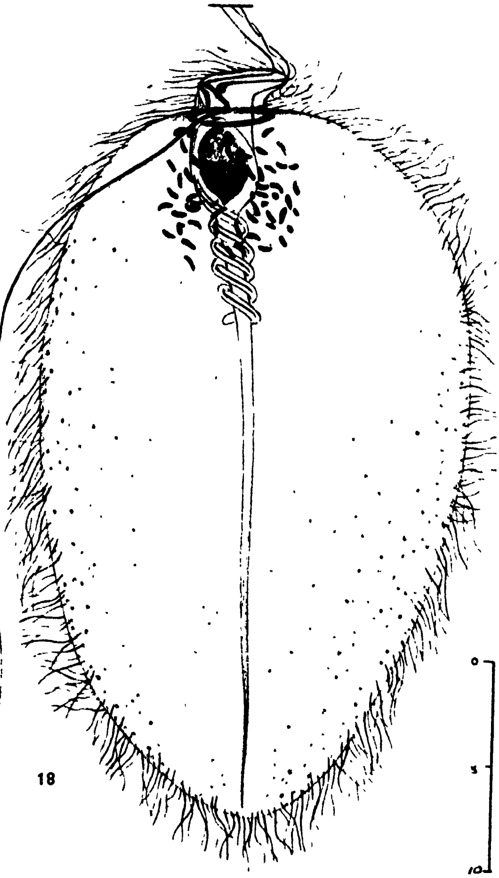

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## PLATE 14

*Caduceia monile* sp. nov. from *Neotermes tectonae.*

Fig. 19. Detail of anterior structures: stopper-shaped protuberance anterior to nucleus, with ring at its base; blepharoplast with a matrix substance in which numerous granules are embedded; deep-staining, large flagellar granule, probably connected by a fine filament to the blepharoplast, but the connection not evident here; anterior extension of capitulum of axostyle; nuclear rhizoplast; parabasal filament; blade-shaped cresta and clavate crestal accessory. S.H. × 3600.

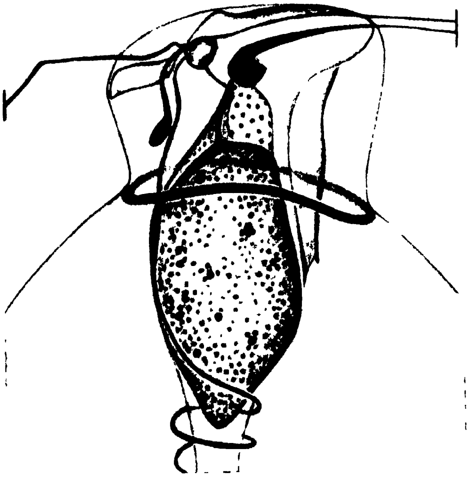
Fig. 20. The end of the crestal accessory extends inside the ring, as is typical; anterior to the nucleus part of the chromatic shield is visible; the parabasal body is turned 12½ times, with the stout parabasal filament at the inner edge. S.H. × 2400.

Fig. 21. Anterior part of parabasal body extended around the nucleus beyond the point closest to the blepharoplast for a distance of half the length of the nucleus. S.D. × 1700.

Fig. 22. Anterior structures showing the overhanging form of the papilla and the groove between the ring and papilla; extension of capitulum on left of nucleus, chromatic shield on right. S.H. × 2400.

Fig. 23. Daughter individual after plasmotomy; the protuberance has not yet developed its characteristic form; the ring is slender; spirochaetes omitted. S.H. × 1400.

Scale × 2400.



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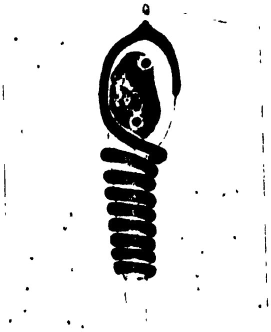

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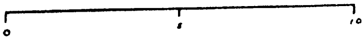

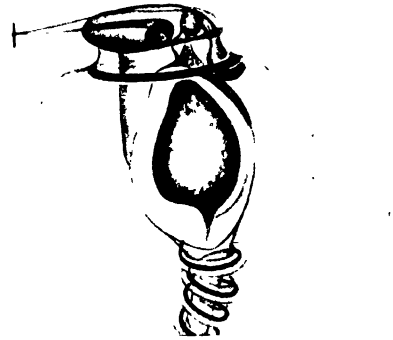

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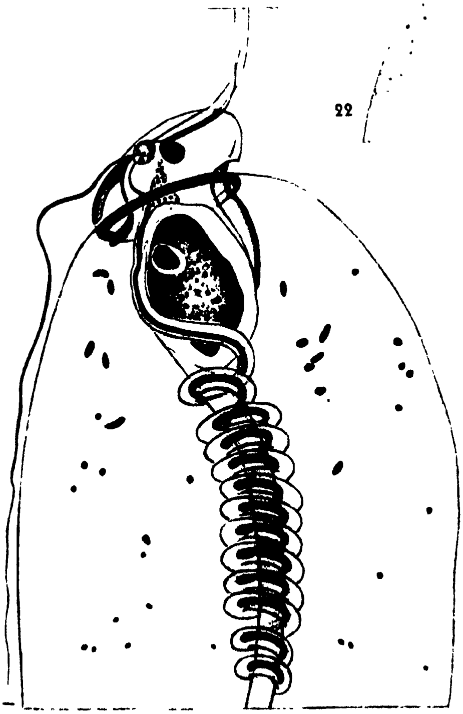

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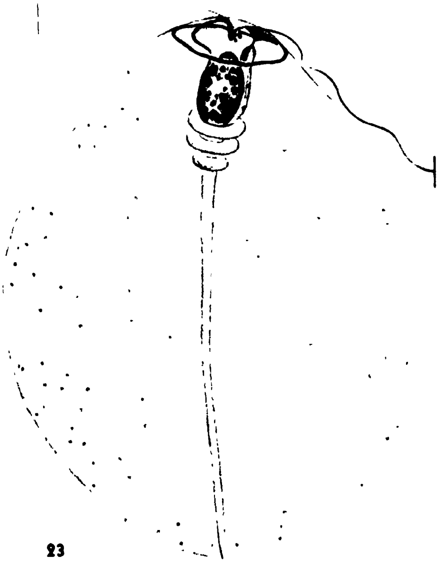

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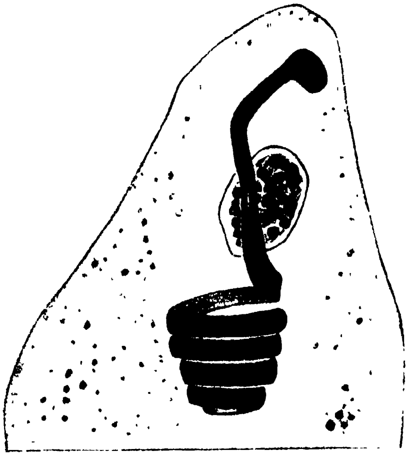
## PLATE 15

*Macrotrichomonas pulchra* Grassi.

Fig. 24. From *Glyptotermes dubius.* Parabasal body with enlargement at anterior end. S.D. × 2330.

Fig. 25. From *Glyptotermes* sp. nov. T-2072, Uganda. Entire: full length of flagella; cresta with denser inner and thinner, undulated outer part; differential stainability in band-shaped trailing flagellum; rhizoplast and suspensorial lamella. S.H. × app. 2400.

Fig. 26. From *Glyptotermes taveuniensis.* Short rods adherent to surface. Holl. H. × 1335.



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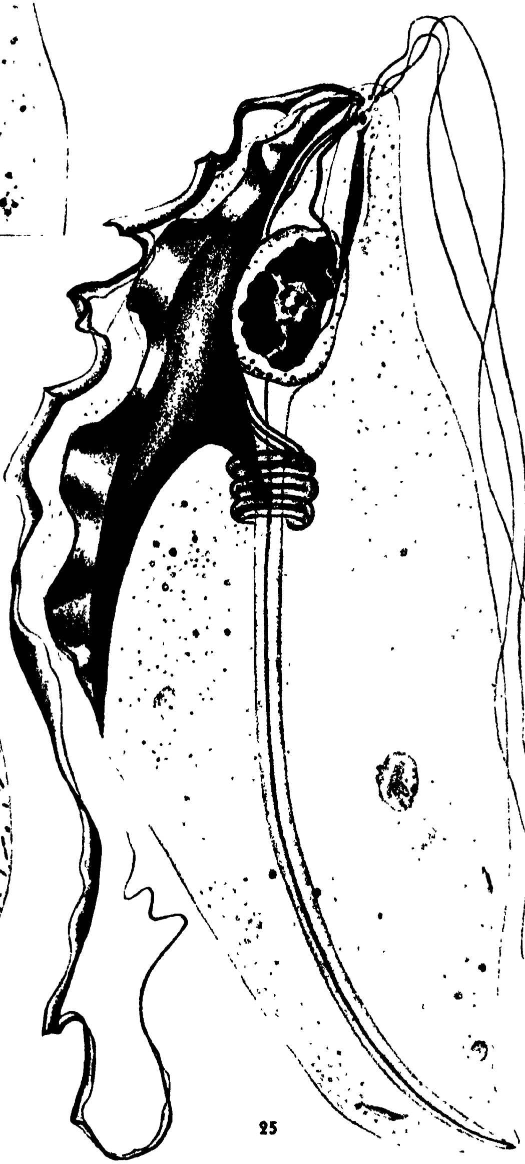

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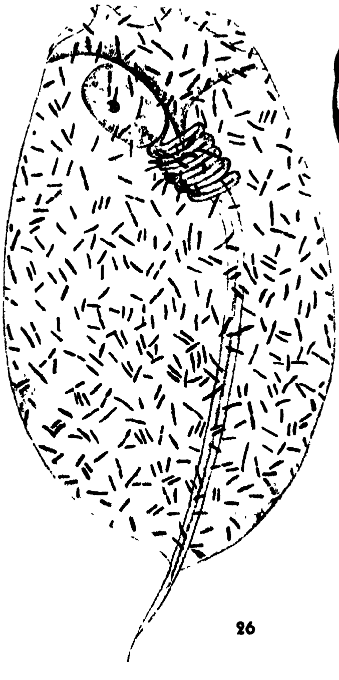

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## PLATE 16

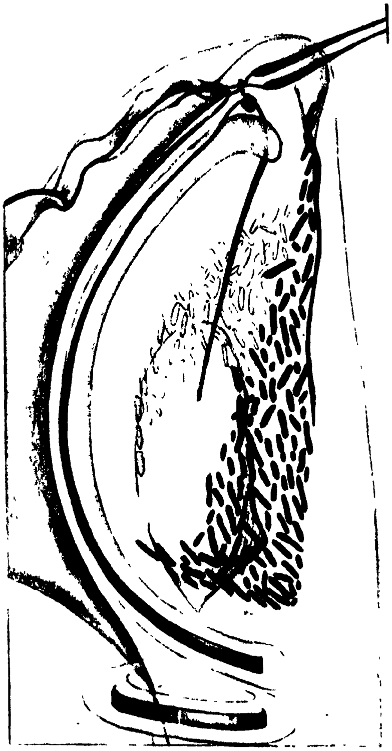
Figs. 27–29. *Macrotrichomonas pulchra* Grassi.

Fig. 27. From *Glyptotermes dubius.* Detail of anterior end. Left to right: trailing flagellum, band-formed with a granulelike terminus connected by a filament to the central blepharoplast; cresta, terminus connected by a filament to the same granule; paracrestal filament closely bordering the cresta; parabasal body, chromophile element band-shaped at the inner edge of the spiral, becoming more slender anteriorly, passing along the longitudinal stouter part of the parabasal, separating from this near the anterior end and apparently connecting to a larger granule posterior to the central blepharoplast; nuclear rhizoplast apparently connected to the same larger granule, but probably extended beyond it to the blepharoplast; two roots of the three anterior flagella with enlarged proximal ends connected by filaments to the central blepharoplast; rods adherent to the capitulum of the axostyle; part of suspensorial lamella on the ventral border of the capitulum. S.H. × 4670.

Fig. 28. From *Glyptotermes* sp. nov. T-2072, Uganda. Similar detail, showing more clearly the granulelike ends of trailing flagellum and cresta, and the filaments attaching these to the central blepharoplast; paracrestal filament, right-angled bend of nuclear rhizoplast; nucleus; capitulum of axostyle, with suspensorial filament along its ventral edge, and optical section of the posterior fold. F.R. × 3470.

Fig. 29. From same host as figure 28. The apparent enlargement of one of the flagellar roots is resolved into the root continuing to the blepharoplast and a rodlike structure alongside it, which is a characteristic structural feature of this species. The trailing flagellum is deeply stained at its inner edge, which is parallel and close to, but not fused with, the external edge of the cresta. F.R. × 3470.

Fig. 30. *Macrotrichomonas unguis* sp. nov. from *Glyptotermes caudomunitis.* A portion of the cresta appears on the right; and paralleling it is the paracrestal filament, which extends inside of the parabasal spiral; at the posterior part of the anteromedial edge of the cresta is the unguis, which here is directed upward and appears as a deeply stained thickening. S.H. × 4670.



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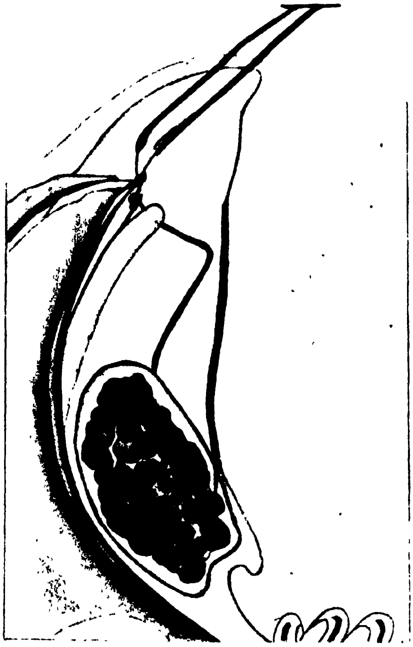

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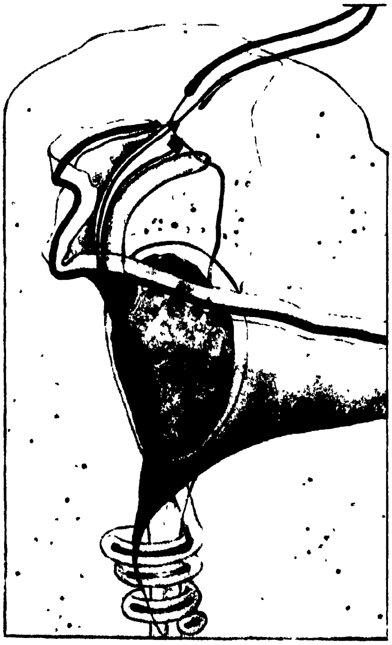

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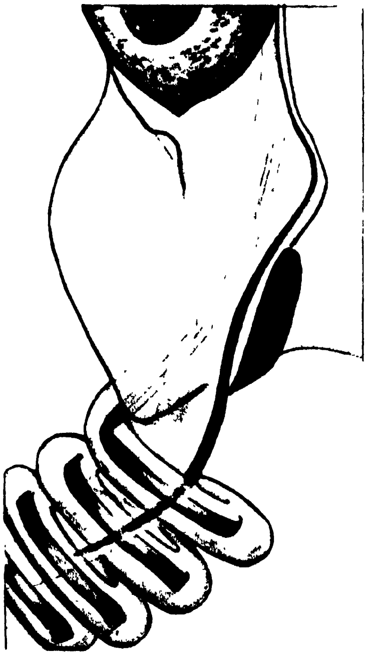

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# PLATE 17

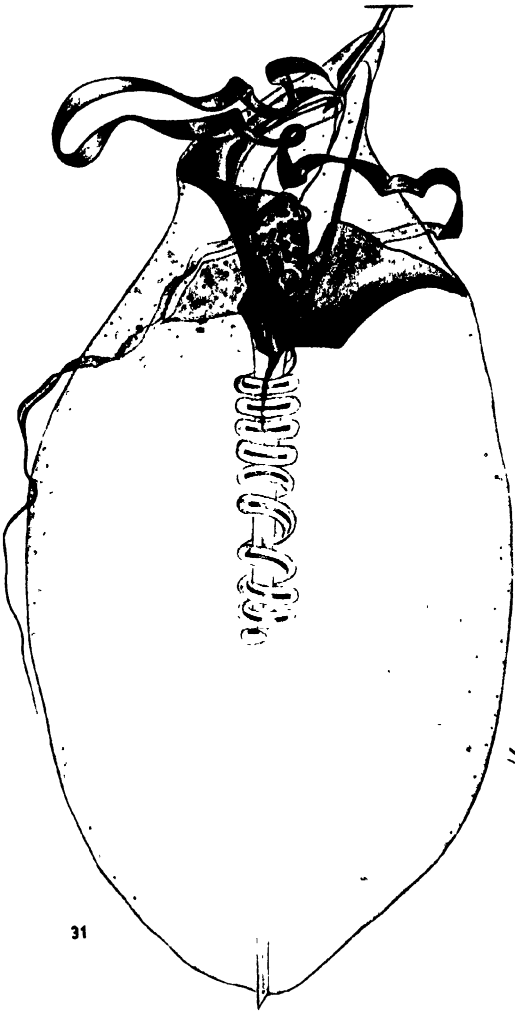
**Figs. 31–33. *Macrotrichomonas unguis* sp. nov. from *Glyptotermes caudomunitis*.**

Fig. 31. Entire: band-formed trailing flagellum separate from edge of cresta, but following it in its transverse turn around the body; the unguis or shelflike extension of the cresta appears at the posterior angle; running beneath it in this figure is the paracrestal filament. Holl. H. × 1700.

Fig. 32. Detail showing the unguis, the concave side of which is here directed upward. Holl. H. × 4670.

Fig. 33. Unusual nucleus, which is reduced to a small size and has a bilobed structure, leaving most of the capitular area unoccupied. S.H. × 2330.

Fig. 34. *Macrotrichomonas unguis* sp. nov. from *Glyptotermes minutus.* The unguis appears as a deeply stained area at the inner angle of the cresta. S.H. × 2400.



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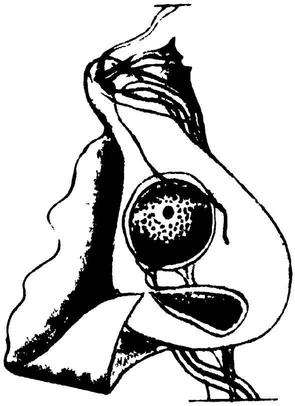

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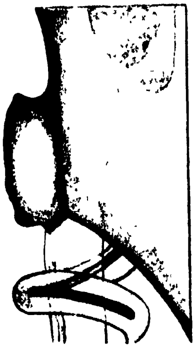

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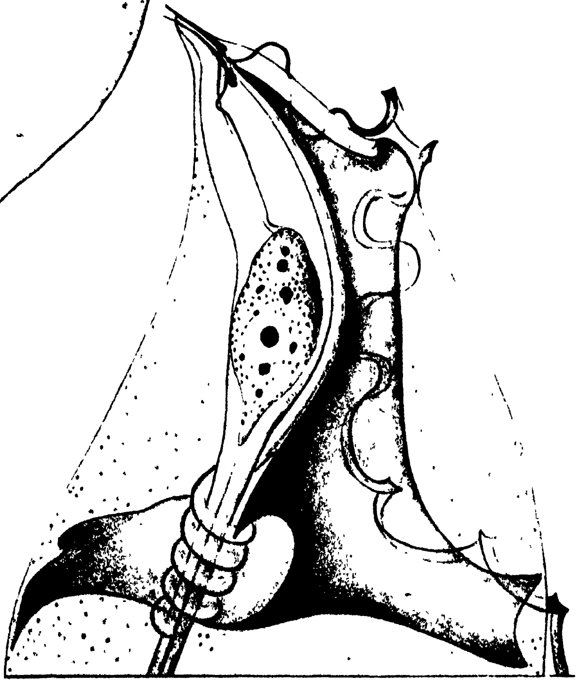

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## PLATE 18

*Macrotrichomonas ramosa* sp. nov. from *Glyptotermes brevicaudatus.*

Fig. 35. Entire: broad, band-shaped trailing flagellum; the parabasal body has a single ramus, arising at the beginning of the spiral. F.R. × 2330.

Figs. 36–45. Parabasal body, with outline of nucleus for position. Various numbers and arrangements of ramus. S.D. × 1770.

Fig. 36. No ramus.

Fig. 37. One ramus, arising near beginning of spiral and curving anteriorly.

Fig. 38. One very short ramus.

Fig. 39. One ramus, rather short, showing manner of origin.

Fig. 40. Two rami, one long, and unusually long hook at the anterior end.

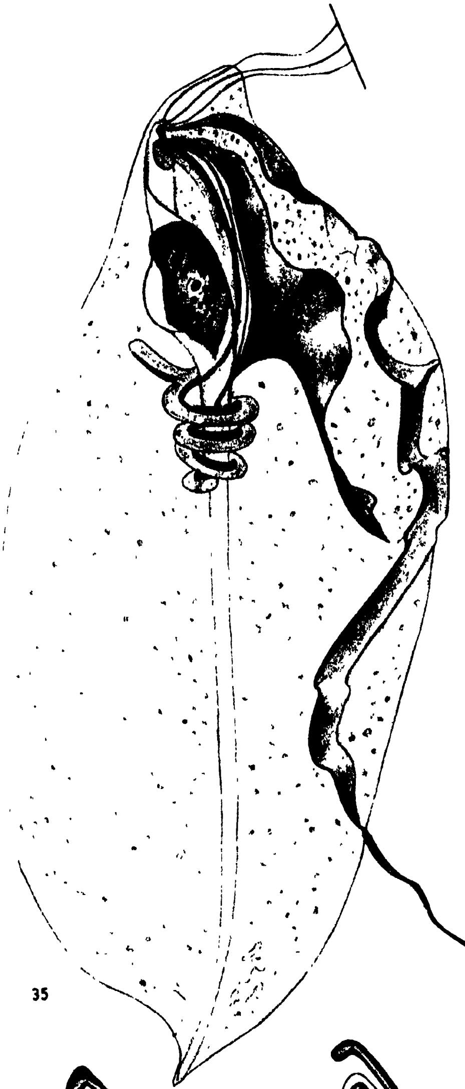
Fig. 41. Three rami, arising close together; two are free and one coils with the spiraled main part.

Fig. 42. Single ramus branched into two, one of which is branched again.

Fig. 43. Two rami, one short and free, one long and coiled most of its length with the rest of the parabasal.

Fig. 44. One ramus as long as the main part and spiraled with it.

Fig. 45. Single ramus, fairly long, spiraled with parabasal as far as it goes.



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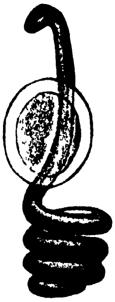

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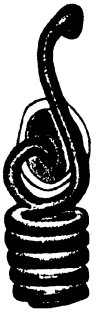

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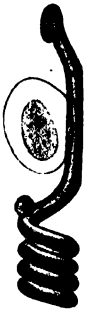

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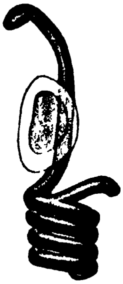

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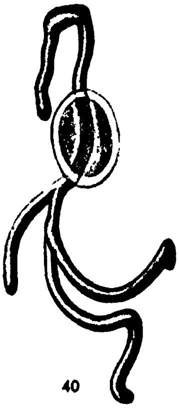

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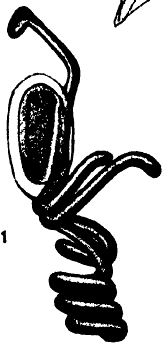

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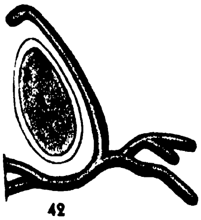

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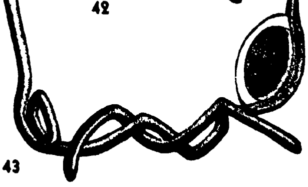

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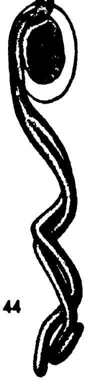

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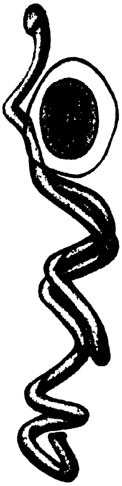

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## PLATE 19

Figs. 46–48. Detail of different parabasal bodies of *Macrotrichomonas ramosa*. S.D. × 4800.

**Fig. 46.** Parabasal appearing cross-banded, alternating stainable and clear areas, both extending completely across.

**Fig. 47.** Anterior end of parabasal, two rows of clear vacuoles in a stained matrix.

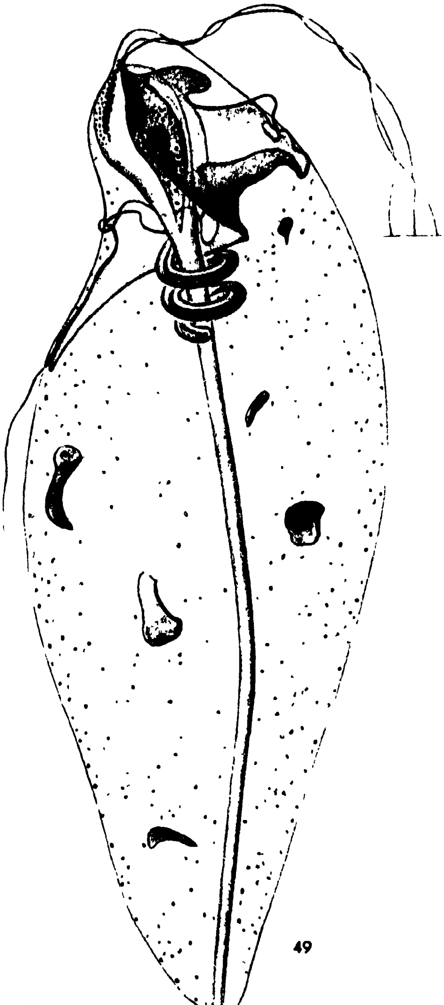
**Fig. 48.** Stainable substance of parabasal in optical section appearing as a series of arms on opposite sides of a central column.

Figs. 49–51. *Macrotrichomonas restis* sp. nov. from *Kalotermes joutcli.*

Fig. 49. Entire, spirochaetes omitted. × 1400.

Fig. 50. Isolated cresta; full length of cordlike trailing flagellum paralleling but not attached to the undulated edge of the cresta. × 2400.

Fig. 51. Parabasal spiral beginning some distance posterior to the nucleus; cresta with deep-staining, thickened inner margin; arm of capitulum, arising in anterior part, turned around trunk of axostyle, narrowed into membrane between the first parabasal turns. Holl. H. × 2330.



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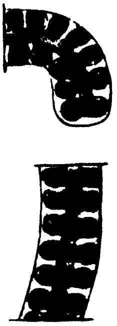

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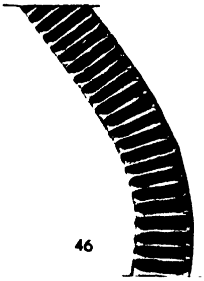

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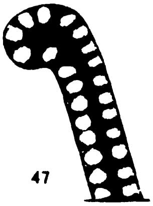

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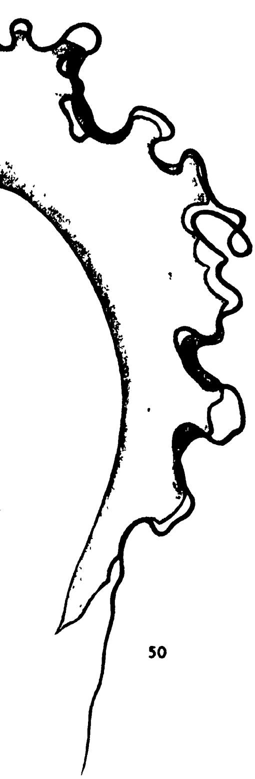

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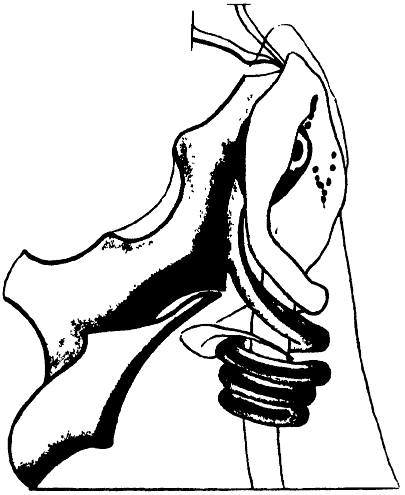

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## PLATE 20

Figs. 52–54. *Macrotrichomonas restis* sp. nov. from *Kalotermes jouteli.*

**Fig. 52.** Forward extension of capitulum of axostyle to one side of nucleus, the trunk of the axostyle not meeting the posterior end of the nucleus; arm of capitulum. Holl. H. × 2330.

**Fig. 53.** Specimen with abnormally small nucleus; trunk of axostyle bending anteriorly and meeting one side of nucleus; anterior extension of capitulum; part of the arm seems here to arise in the posterior part of the capitulum. Holl. H. × 2330.

**Fig. 54.** Parabasal body, showing the bandlike chromophile element and the curved anterior part on the anterior surface of the nucleus. C.H. × 2330.

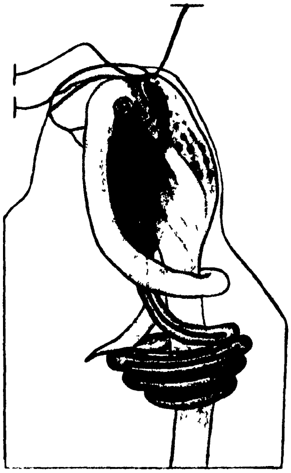
Figs. 55–58. *Macrotrichomonas virgosa* sp. nov. from *Procryptotermes* sp. nov. T-4359. Madagascar.

**Fig. 55.** Stained, riblike inner margin of cresta, and undulatory outer part; trailing flagellum closely following the external edge of the cresta; papillar granules in three rows between the blepharoplast and the tip of the papilla; parabasal spiral beginning immediately posterior to the nucleus. Holl. H. × 2330.

**Fig. 56.** Arm of capitulum, originating anteriorly, extended in a troughlike membrane within the first turn of the parabasal body. Holl. H. × 2330.

**Fig. 57.** Parabasal body; more turns of the spiral than usual. S.D. × 2330.

**Fig. 58.** Parabasal body; forward-extending conical structure at anterior end; one short ramus arising from the first part of the spiral. S.D. × 2330.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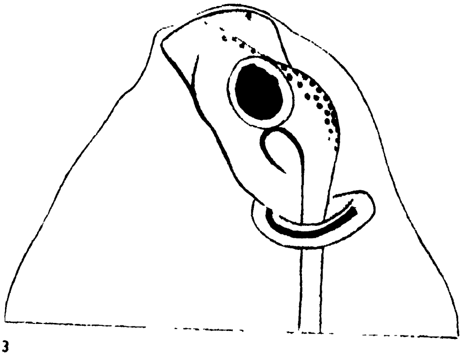
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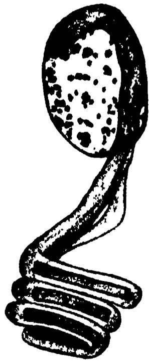
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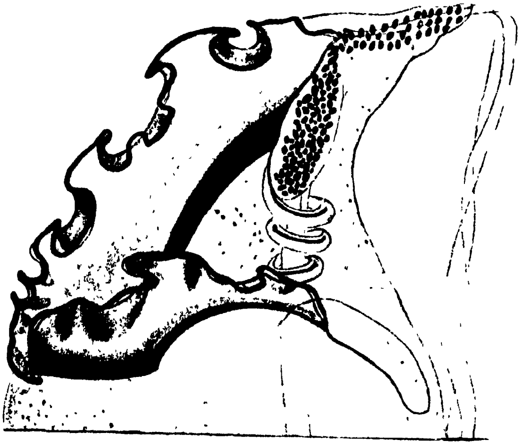
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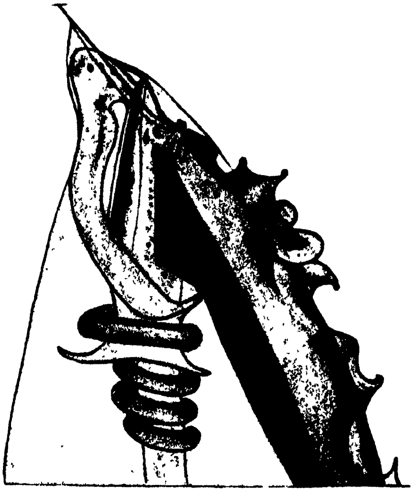
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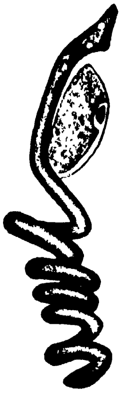
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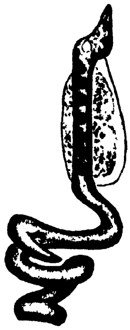
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## PLATE 21

*Macrotrichomonas virgosa* sp. nov.

Figs. 59–63. Parabasal bodies. S.D. × 2330.

**Fig. 59.** Anterior part moniliform, conical anterior extension attached to rest by a narrow margin.

**Fig. 60.** Anterior part, conical end attached to rest by a filament; some small vacuoles in the parabasal substance.

**Fig. 61.** Anterior part, broken into sections; these are probably connected by a substance that is not evident in Delafield-stained material.

**Fig. 62.** Form of parabasal body in the majority of specimens.

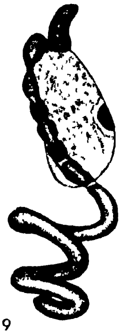
**Fig. 63.** One long ramus arising at beginning of spiral.

Figs. 64–66. Adherent rods. Holl. H.

**Fig. 64.** Many of the rods detached from the cup-shaped structures in the cytoplasm. × 2330.

**Fig. 65.** Rods resting in the cytoplasmic cuplike structures, from which only a few are detached. × 2330.

**Fig. 66.** Semidiagrammatic, showing the detailed structure of the rods and the stainable bodies at the ends in the cytoplasm. × 4670.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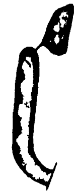
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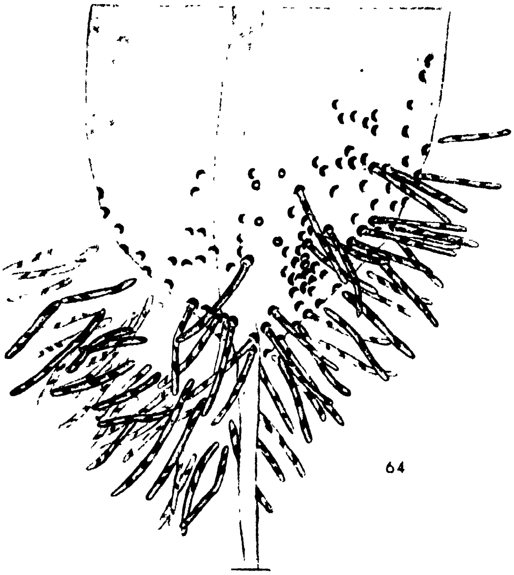
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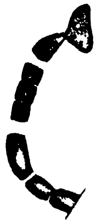
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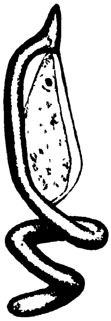
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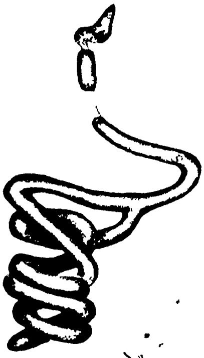
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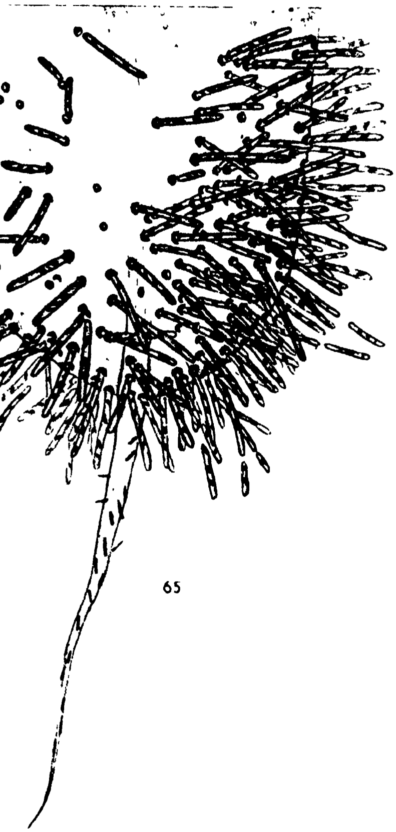
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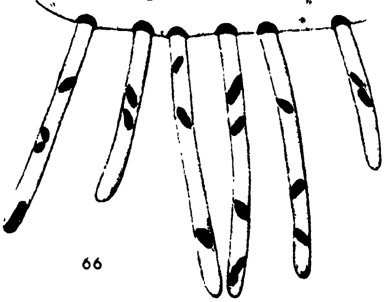
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## PLATE 22

Fig. 67. ***Macrotrichomonas procera*** sp. nov. from *Calcaritermes* ***brevicollis.*** The relatively long region anterior to the nucleus is characteristic of the species. Drawing combined from two specimens. S.D.F., S.H.F. × 2400.

Figs. 68–72. *Macrotrichomonas lighti* (Connell) from *Paraneotermes simplicicornis.*

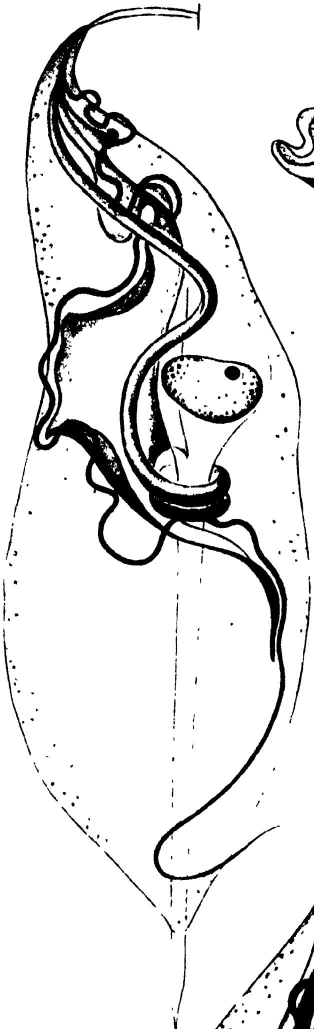
Fig. 68. Detail: anterior granules and attachment of organelles; anterior end of parabasal and parabasal filament; nuclear rhizoplast bent at right angle; suspensorial lamella on ventral side of capitulum. Zirkle's copper dichromate fixative. H. × 2400.

Fig. 69. Entire: the trailing flagellum is more band-formed than was shown by Connell, and is not fused to the cresta. C.H. × 1400.

Fig. 70. Cresta; thickened ribs along the anteromedial and posteromedial edges, with bulbous enlargements of each at the angle where these edges meet;, band-formed trailing flagellum adherent to the external edge of part of the cresta, although the cytoplasm of the body has been destroyed. × 1146.

Fig. 71. Cresta turned transversely around nucleus. The rib of the posteromedial edge appears posterior, and its projection beyond the thin membranous part shows in side view. The trailing flagellum adheres to the edge in part, although the cytoplasm has been dissipated. × 1146.

Fig. 72. Edge of a part of the cresta of figure 70, showing the striations perpendicular to the edge, on the membrane. In the upper part of the figure they are seen in end view, below in flat view. × 2330.



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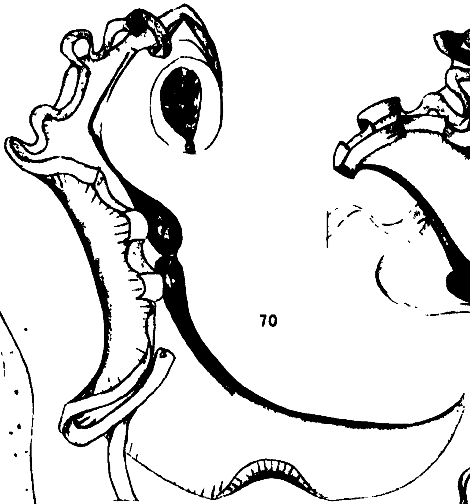

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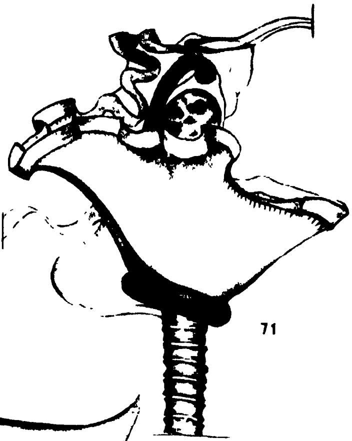

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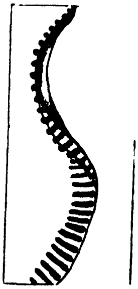

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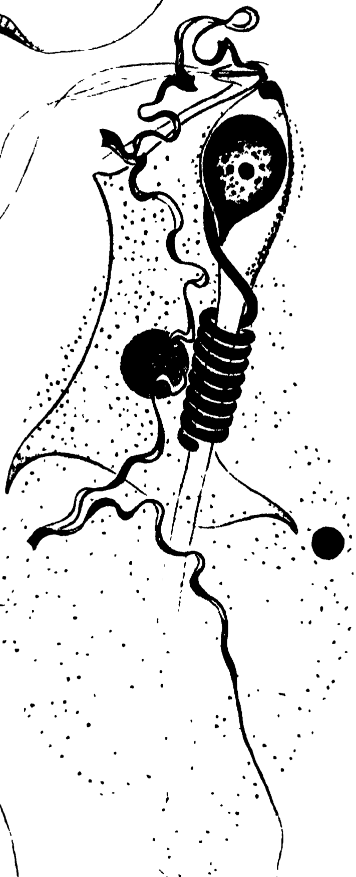

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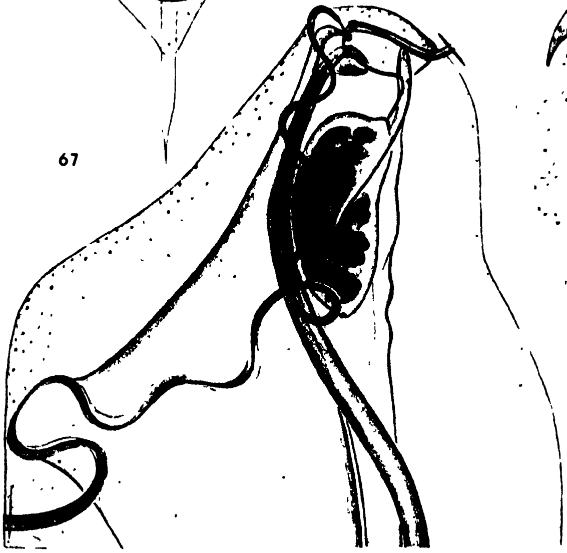

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# DEVESCOVINID FLAGELLATES OF TERMITES

# III. THE GENERA FOAINA AND PARAJOENIA

BY

HAROLD KIRBY

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# DEVESCOVINID FLAGELLATES OF TERMITES

# III. THE GENERA FOAINA AND PARAJOENIA

BY

HAROLD KIRBY

## DESCRIPTIVE AND SYSTEMATIC ACCOUNT

### GENUS FOAINA JANICKI

### **Foaina** Janicki

*Foaina* Janicki, 1915, Zeitschr. wiss. Zool., 92:615; type species, *F. gracilis* Janicki.
*Janickiella* Duboscq and Grassé, 1923, C. r. Acad. Sci., 177:178; type species, *J. grassii* Duboscq and Grassé.
*Paradevescovina* Kirby, 1926, Univ. Calif. Publ. Zoöl., 29:114; type species, *P. nana* Kirby.
*Crucinympha* Kirby, 1938, Quart. Jour. Micr. Sci., 81:9; type species, *C. hilli.*

*Diagnosis.*—Size small to moderate, average length in known species ranging from 10 to 38 (48)μ, complete range 6–54 (69)μ, average width 5–19 (25)μ, complete range 3–31 (40)μ; three long, slender anterior flagella; trailing flagellum usually exceeding twice the length of the body, varying in development from a thickness little more than that of an anterior flagellum to that of a stout cord or a ribbon; cresta, in direction vertical to surface of body, usually very slender, moderately broadened anteriorly, tangential to surface often narrow band-formed, length in known species 1.5–29μ, averaging 2.5–17μ, reaching to the posterior end of the body in some instances; parabasal body single, in some species with one or more rami, ranging from an ellipsoidal or bacilliform structure shorter than the nucleus to a longer structure curved around the nuclear membrane or in its distal part extended toward the periphery of the body, but not coiled around the axostyle, parabasal filament often extending free beyond the main substance; capitulum of axostyle varying from a simple expansion to a broadened, curved membrane, capitular granules abundant in some species, few or none in others; trunk of axostyle not tapered greatly within the cytoplasm; projecting cusp expanded or not, varying in different species and within the species; siderophile rings or a band sometimes present around the trunk before projection of the cusp; longer diameter of nucleus, in reference to position of blepharoplast, usually transverse or oblique, in several species more or less flattened and curved in a transverse or oblique direction; chromatin mass of nucleus typically finely granular, destaining readily after iron-haematoxylin, with usually one or two deep-staining peripheral nucleoli, and usually no clear space between the membrane and the mass; no *Fusiformis*-like organisms regularly adherent to the surface; spirochaetes adherent to parts of the body or the entire surface of some species, but usually absent.

#### TAXONOMY AND DISTRIBUTION

Janicki's diagnosis of the genus *Foaina,* which he named for Dr. Anna Foà, is as follows: Elongated or oval forms with three flagella, which arise from a blepharoplast situated asymmetrically at the side in the anterior part of the body; a trailing flagellum is present. Parabasal apparatus consisting of two parabasal bodies embracing the nucleus, axostyle present. Type species, *F. gracilis* Janicki, in hindgut of *Calotermes castaneus* Burm. (Honolulu). (Host actually *Neotermes connexus* Snyder.)

This diagnosis is applicable to any devescovinid, as well as to *Monocercomonas* (*Eutrichomastix*), except for the supposed double parabasal apparatus. In this point, however, the diagnosis is incorrect, as I have shown (1938*b*), and therefore valueless.

The fact that *Janickiella* is a synonym of *Foaina* was remarked by me in an earlier paper (1937*a*), as well as in the first part of this monograph. The reasons will be apparent if the account of *F. grassii*, the type species of *Janickiella* (p. 179), is compared with that of *F. gracilis* (p. 190, and Kirby, 1938*b*). The status of *Janickiella* has been a confused one. Duboscq and Grassé (1923) noted the resemblance to *Eutrichomastix*, and later (1924), when other small polymastigotes of *Kalotermes flavicollis* were included in the supposed cycle of *J. grassii*, they designated the typical forms as the *Eutrichomastix* stage. As described in their two papers, the structures correspond to those of *Foaina gracilis*, except that the parabasal apparatus was then erroneously supposed to be double in the latter flagellate. Except for a second species of *Foaina*, originally described as *Trichomonas dogieli*, there is no other devescovinid in *Kalotermes flavicollis*. This obviated the error, later made by Duboscq and Grassé, of confusing flagellates of the same type with supposed developmental stages of larger devescovinids.

De Mello (1932) described as *Janickiella duboscqi* a small flagellate from the intestine of the lizard *Hemidactylus brookei*. He stated, however, that the cresta does not exist in the flagellate; and in the absence of the cresta, which is characteristic of all devescovinid flagellates, there appears to be no valid reason for not assigning the flagellate of *Hemidactylus* to the genus *Monocercomonas* (*Eutrichomastix*).

In 1926 I described *Paradevescovina*, with the genotype *P. nana*, and stated that it closely resembles *Devescovina* but is distinct from it in the parabasal body. Only the chromatic filament of the parabasal body was seen by me then. The course of this filament is certainly different from that in *Devescovina*, but the parabasal apparatus is related to the type of parabasal in *Foaina gracilis* and *F. grassii* through the series of forms now known. Duboscq and Grassé (1929), noting the similarity of the parabasal of *"Paradevescovina"* to that of certain forms of *Janickiella* (*"Trichomonas dogieli,"* which they then supposed to be a phase of development of *J. grassii*), expressed their belief that the two genera had been confused.

In 1938 I established the new genus *Crucinympha* for the flagellate of *Glyptotermes iridipennis* named *Devescovina hilli* by Duboscq and Grassé (1926). The distinction rested on what was supposed to be the uniqueness of the parabasal body. The series of forms in the genus *Foaina*, as described in this paper, relate the parabasal of *Crucinympha* to more typical parabasals of *Foaina*, and indicate that *Crucinympha* cannot be separated from *Foaina* unless a number of other forms with branched parabasals are similarly treated. Branching of the parabasal is, however, found in all other genera of Devescovininae, and subdivision on this basis alone is impossible. *Crucinympha* is considered to be a synonym of *Foaina*.

Grassé (1938) stated that *Foaina* of Janicki is a synonym of *Parajoenia*.

Nevertheless, because of certain unique features in the organization of *Parajoenia* it seems best to retain it and *Foaina* as independent genera. This point is discussed in the account of *Parajoenia grassii* (p. 121).

In the records that follow, twenty-six species of *Foaina,* nineteen of them new, are described from termites of the large former genus *Kalotermes* (s. lat.) and *Anacanthotermes ochraceus.* I found *Foaina* in all but 39 of 132 species of Kalotermitinae, which were separated partly according to species determinations and partly, when such determinations had not been made, according to flagellate faunules. Forty-four hosts contained only one species, 42 had two species, and 3 had three species. In four of the hosts the species of *Foaina* were not determined because of poor preparations or inadequate material, though at least one was present in each. Published records indicate the presence of at least one species of *Foaina* in each of two other species, which I have not examined.

Janicki (1915) remarked that *Foaina gracilis* was usually rare in its host but occasionally occurred in large numbers. I have observed this variability in abundance not only in *F. gracilis* but also in several other species of the genus. It is worth noting because of the contrast to *Devescovina, Macrotrichomonas,* and *Metadevescovina,* which occur in more constant numbers. There is no obvious reason for this difference and it is here stated only as an observed fact. *Foaina reflexa,* a common and widespread species, was often abundant on only a small number of slides in a series. *F. ovata* from *Neotermes howa* and *F. taeniola* from *Paraneotermes simplicicornis* were comparatively rare in the material examined. Species of *Foaina,* like certain other flagellates in termites at times, were occasionally found to be absent from some colonies of a host species and present in others; or they were consistently abundant in one group and infrequent in another. In the great majority of instances, however, the species entering into the composition of the faunule of a host species were present in abundance in each individual termite.

In regard to the suggestion which has been made that flagellates of the type designated here as *Foaina* may be developmental forms of larger devescovinids, their associations are significant. In some hosts species of *Foaina* are present unaccompanied by larger devescovinids. These are *Kalotermes flavicollis, Neotermes howa, N. howa* var. *mauritiana, N. gracilidens, N. amplus,* and *N. desneuxi.* In many other termites the associated devescovinid is a large form that cannot possibly be regarded as related ontogenetically to the species of *Foaina* present. Devescovinids in a considerable number of hosts are unaccompanied by *Foaina.* Species of *Devescovina* in Kalotermitinae have always been found with one or more species of *Foaina,* but there are many different combinations of species of the two genera.

## GENERAL MORPHOLOGY

The genus *Foaina* includes the smallest Devescovininae, but some species are larger than certain small species of *Devescovina.* In the diagnosis the dimensions of the unusually large species *F. ramulosa,* which greatly increase the range, are put in parentheses. With the inclusion of this species the length ratio ranges from 1 to 11; without it, from 1 to 8; whereas the averages are about 1–4 and 1–5, respectively. This size range, although large, is not so great as that of species in the genus *Trichomonas;* and is not greater by any considerable amount than that to be observed in the one species *Trichomonas termopsidis* (Kirby, 1931*a*, pp. 184, 220).

Janicki described as follows the characteristic body form of *Foaina gracilis:* Rounded anteriorly, somewhat asymmetrical, the middle part of the body a little broader than the anterior end; a lateral indentation between the anterior and middle parts of the body, on the side where the blepharoplast is located; not sharply pointed posteriorly, with the axostyle usually projecting. *F. gracilis* has a stouter body form than some species of the genus, but the broad body form characterizes most species of *Foaina.* When the papilla is extended, the rounded form of the anterior end is altered, as in *Devescovina;* but the papilla is more prominent in some species than in others. There is a distinct difference from the usual form of *Devescovina* in the absence of the elongated, pointed posterior end, and in the presence of a projecting cusp of the axostyle.

In the region of the papilla there is in certain species a conspicuous, elongated, clear area (pl. 24, figs. 21, 22) evidently homologous with the so-called cytostome of *Trichomonas.* This clear area extends between the anteroventral edge of the capitulum (blepharoplast dorsal) and the margin of the papilla (fig. A, 11). It is not very evident in some other species, so that it is a characteristic of some taxonomic value.

The anterior flagella are fairly uniform in relative length in the different species, often measuring about 15–20$\mu$ in the small ones and 30–35$\mu$ in the larger ones. Duboscq and Grassé (1923) recorded the length as 20$\mu$ in *F. grassii;* de Mello and de Brito (1929) reported 20–25$\mu$ in *F. nana* (*"Devescovina kirbyi"*). For at least part of their length the three flagella are united.

The trailing flagellum is always longer and usually is considerably stouter than an anterior flagellum. The great length of this is typically a point of distinction from other genera of Devescovininae. It generally exceeds twice the length of the body (fig. C, 1), the exceptions being in *F. pectinata* and large individuals of certain species, and often it is three or four times this length, or even more (pl. 23, fig. 2). In *F. solita* a length of five times that of the body was recorded.

The trailing flagellum is always very slender at the proximal and distal ends (fig. B, 6). In a few species (*F. dogieli, F. parvula, F. humilis,* and *F. pectinata*) it is slender for its whole length. Usually, however, it enlarges to a cord, and occasionally it is flattened. A band-formed trailer is less frequent than in *Devescovina.* When the trailing flagellum is stout it is often somewhat flattened (*F. hamata*), but a well-developed ribbon form was observed in only one species (*F. taeniola,* fig. A, 7).

As in *Devescovina,* the breadth of the trailing flagellum is somewhat variable within a given species; furthermore, the apparent size varies with the depth of the stain. Both types of intraspecific differences are limited in extent, however; and they do not preclude use of this characteristic of size of the trailing flagellum in taxonomy. The characteristic is particularly useful if the entire range of variation can be taken into account. This it has often been possible for me to do because of the large number of host infections studied.

The trailing flagellum normally adheres to the surface of the body for the length of the cresta; this I observed in living material of *F. dogieli, F. grassii, F. exempta,* and *F. costata.* The insecure nature of the attachment is discussed in the accounts of *F. costata* (p. 194) and *F. dogieli* (p. 195). It is possible to understand why Duboscq and Grassé considered the cresta and flagellum of *F. dogieli* to represent a true undulating membrane, since they then knew only that species and *F. grassii;* but consideration of abundant comparative material obviates such an error of interpretation. The adherence is apparently of the same character as that of the anterior flagella to the papilla.

The activity of the flagella is described below in the accounts of *F. grassii* (p. 180), *F. exempta* (p. 188), and *F. costata* (p. 194). As in other devescovinids, the anterior flagella are chiefly responsible for the locomotor movements of the body, and one does not see such vigorous undulations of the trailing flagellum as occur in the undulating membrane of *Trichomonas.* The maintenance of a long spiral form by that flagellum, as was observed in *F. exempta,* is particularly interesting (p. 188).

The blepharoplast is a compact structure, which in well-stained material usually appears as a single body. Duboscq and Grassé's statement (1923) that in *Janickiella grassii* there is a large blepharoplast giving rise to the trailing flagellum and close to it a smaller granule giving origin to three anterior flagella was not corroborated by their later report (1924), in which figures were given. In some larger species the blepharoplast can be resolved into a number of granules (pl. 27, figs. 39, 41), but the structure is less complex than in some higher Devescovininae. Departure from the simple, compact form was seen only in the irregular posterior prolongation in *F. ramulosa* (p. 218).

The cresta varies greatly in length within the genus, from a very small structure difficult to detect to a rod extending the full length of the body and resembling a well-developed costa of *Trichomonas* (fig. A, 11). The anterior end of the cresta is always expanded. The anteromedial edge seldom has a length in excess of $1\frac{1}{2}\mu$, even in large species, whereas in *Devescovina* it often exceeds $2\mu$. No such expansion of the anterior end has been observed in the costa of *Trichomonas.* In some species, such as *F. hamata,* the cresta tapers gradually to the posterior end (pl. 26, fig. 32); but often, just beyond the expansion, it diminishes abruptly to a slender rod that continues in a uniform size (pl. 29, fig. 50).

The crestal shape described in the preceding paragraph is that observed when the body is oriented so that the cresta is at one edge. The cresta appears, ordinarily, very dark in well-stained iron-haematoxylin preparations. When the body is so oriented that the cresta is above, it can often be observed that the cresta is band-formed, with no expansion at the anterior end in this direction. It then appears less darkly stained, as the material of the cresta is then not so deep. This band form has been observed in many species. It was most clearly seen in *F. costata,* in which its breadth of about $\frac{2}{3}\mu$ is the maximum observed in the genus (pl. 25, figs. 28, 29).

The parabasal apparatus is very simple in structure in several small species (*F. grassii, F. solita, F. parvula*), in which it is an elongated, usually bacilliform body on the dorsal side of the nucleus, between that body and the cresta (fig. A, 1–3). Its end is attached to the blepharoplast, with no part extending anteriorly beyond the blepharoplast. Such a parabasal body is like that of species of *Monocercomonas* (*Eutrichomastix*) and the simpler forms of *Trichomonas.*

The parabasal body is relatively longer in larger species. It does not, however, extend posteriorly as a straight body, beyond the posterior level of the nucleus; when it reaches this point it turns transversely or obliquely across the nuclear membrane (pl. 26, fig. 33). At the anterior end it often extends beyond the point nearest to the blepharoplast. The result of this development may be a C form applied to the nuclear membrane, a form that is notably achieved in *Foaina gracilis* (fig. A, 9); or the posterior part may extend beyond the lateral limits of the nucleus, as in *F. falcifera* (pl. 27, figs. 39–41) and other species. The distal part of the parabasal body of the latter type is sometimes curved more or less anteriorly again; the extreme in this development is found in *F. reflexa,* in which there is a sharp bend anteriorly following the proximal, longitudinal part (pl. 28, figs. 45, 46). The form of the parabasal body, though somewhat variable within a species, has characteristics that are of considerable taxonomic value.

The parabasal filament extends along the edge toward the nucleus, and continues, often, beyond the end of the other substance. This free filament is particularly long in *F. nana* and *F. costata,* in which it follows the margin of the body posteriorly for some distance (pl. 25, fig. 28). The filament is obscure in the proximal part of the parabasal, and it has seldom been possible, in this genus, to determine the connection to the blepharoplast. In *F. hamata* and some other large forms, however, it has been ascertained that the attachment is like that observed in many other devescovinids. The filament separates from the other substance, which may continue anteriorly around the nuclear membrane, and joins the blepharoplast directly (fig. B, 3, 6, 7; pl. 26, fig. 35).

Outgrowth of rami of the parabasal apparatus takes place in certain larger species. There is only one outgrowth in *F. appendicula* (pl. 29, fig. 50) and *F. duo* (pl. 29, fig. 53); one or two in *F. hilli* (fig. C, 4); several separate ones in *F. nucleoflexa* (fig. E) and *F. pectinata* (pl. 31); and a branched ramus in *F. ramulosa* (pl. 30, figs. 61, 63).

Heterogeneity in the substance of the parabasal can be seen in some larger species, but it is not so marked as in certain species of *Metadevescovina.* Occasionally a row of deep-staining granules appears (pl. 27, fig. 40); more commonly there are a number of clear vesicles, in one or two rows or irregularly arranged.

The capitulum of the axostyle is usually a moderately expanded, flat structure alongside the nucleus and extended into the papilla. Its oblique anteroventral margin is in many species separated from the margin of the body by the clear space that has been mentioned before. A rather elaborate expansion and curvature of the capitulum, rendering it comparable to that in *Meta-*

*devescovina debilis* and some other species of that genus, has been observed in *Foaina nucleoflexa* (p. 217).

Duboscq and Grassé described "frontal granules" in the anterior region of *Janickiella grassii* and *"Trichomonas" dogieli* (1923, 1924). Those of the former species, they stated, are disposed in two arcs; in the latter they form an extensive triangular field anterior to the nucleus. I have observed these granules in many species of *Foaina.* They are more abundant in some species than in others—a circumstance illustrated by the two species described by Duboscq and Grassé. They are restricted to the area occupied by the capitulum, and seem to be situated on the capitular membrane. For this reason I use the term "capitular granules" instead of "frontal granules." A row of these granules follows the margin of the capitulum. The number of granules present in different individuals of a species often varies, as is noted below (p. 217) in *Foaina nucleoflexa.* Although the spherical granule form is usual, many of those in *F. ramulosa,* and apparently all those in *F. nucleoflexa* (fig. E, 9), were observed to be short rods.

The trunk of the axostyle is a stout rod extending through the cytoplasm in a straight or slightly curved course. Because the axostyle does not become filamentous within the cytoplasm, it is never sinuous in its posterior part, as it often is in *Devescovina.* Instead, there is only a little decrease in diameter from the part near the nucleus to the posterior end of the body. There is then always a terminal cusp that projects from the body, tapering to a point and often prolonged in a filament (pl. 30, fig. 65; fig. B, 1). The projecting cusp is not invested in cytoplasm. That fact is easily determined in larger species, but it is true also in all other species, contrary to the account of *Janickiella grassii* by Duboscq and Grassé (1924).

The trunk of the axostyle appears undifferentiated in small species, but in larger ones there is distinguishable an outer sheath and a core, between which, for most of the length, there is a narrow space (fig. C, 5). This space broadens at the anterior end, as the core does not enlarge markedly. The sheath is expanded as the membrane of the capitulum. Often at the posterior end of the cytoplasm the sheath again expands, and may reach twice the diameter of the preceding part of the trunk, giving an enlarged, spearhead-formed cusp (fig. B, 6). There may be a sharp angle at the broadest part of the cusp; or it may be more smoothly rounded (*F. nucleoflexa*). This angle may coincide with the limits of the cytoplasm (*F. hamata*). The core of the axostyle tapers gradually, undergoing no enlargement whether or not the sheath is posteriorly expanded.

In some species an enlargement of the cusp has never been observed (*F. nana*), whereas in others there seems always to be such an enlargement (*F. minuscula, F. hamata*). The presence or absence of such an enlargement, however, is not a simple criterion of species distinction, for in some species both conditions occur (*F. reflexa,* in the account of which, page 209, this variation is discussed). When the enlarged cusp is consistently absent or consistently prominent, however, it is a characteristic of use in recognition of species.

From the beginning of the enlargement to the point of greatest diameter there sometimes appears a deep-staining muff, or band, around the trunk of the axostyle. It could not be decided whether this is a surrounding structure or merely a thickening of the membrane. The band has been seen particularly well in *F. hamata* and *F. minuscula.*

Some species show one, two, or occasionally more, close-fitting rings around this region of the trunk of the axostyle (fig. A, 7; B, 4; pl. 23, fig. 4). The presence of these, even more than that of the band, should be a valuable characteristic for classification; but demonstration of the rings is dependent upon fortunate staining conditions. In species known to have them they may not be seen on whole series of slides.

The nucleus of *Foaina gracilis,* which was accurately described by Janicki (1915, p. 616), is typical of the genus. He noted the elongation in the transverse direction; this is carried to the most marked extent in *F. funifera* (fig. B, 10). Occasionally, however, the direction of the elongation is not transverse, but longitudinal, as in *F. hamata* (pl. 26, fig. 32). In some species the entire nucleus is curved in a transverse direction, as in *F. funifera, F. reflexa,* and, especially, *F. nucleoflexa* (fig. E, 7, 8). This curvature is a very marked characteristic of the last-named species, in which the nucleus is also markedly flattened, especially in its proximal part.

Janicki noted the large, round Binnenkörper, surrounded by a vacuole, and the finely granular chromatin. The material filling the nucleus loses haematoxylin stain much more readily than does that of *Devescovina,* so that on the same slide the nucleus may be much paler. The nucleolus-like body, however, retains the stain tenaciously. This body is situated at the periphery of the nuclear mass, and is separated by a clear area. Sometimes there are two or three such structures. In *F. exempta* the nucleus is unusual in the presence of a larger number of granules at the periphery (p. 188).

A body much larger than the nucleolus, situated in the ground substance of the nuclear mass, and containing several granules, is a unique characteristic of *Foaina signata* (pl. 26, fig. 36).

Janicki observed that there is no space between the membrane and the chromatin mass in the nucleus of *Foaina gracilis.* This, he stated, constitutes a difference between the nucleus of *Foaina* and that of *Devescovina.* I have pointed out in this monograph that the space, resulting probably from technical treatment but nevertheless representing a structural difference, is not always present in *Devescovina;* and that sometimes, furthermore, a space is present in *Foaina* (*F. signata*). It is, however, very unusual in the latter genus.

Janicki (1915) noted that *Foaina gracilis* almost always contains rounded inclusions that become brown when treated with osmic acid and which stain deeply with iron-haematoxylin (fig. A, 8). By these inclusions it was possible for him to differentiate quickly between that flagellate and *Devescovina.* The spherules are characteristically present in many or most individuals of certain species of *Foaina,* such as *F. exempta* (fig. A, 5), *F. solita, F. humilis, F. taeniola, F. ovata, F. gracilis, F. grassii,* and *F. parvula.* They seem to be absent altogether from some other species, as they are from *Devescovina.*

It is possible that the differences among species in types of inclusion indicate some difference in habits of nutrition. Particles of wood were not observed in

*F. exempta,* for example, in which the spherules are abundant. In some other forms, however, wood particles were observed along with the spherules (fig. A, 7). Fragments of wood are numerous in the cytoplasm of some species of *Foaina;* and probably all species ingest wood.

All species of *Devescovina* have a consistently "striated" body surface, owing to the presence of *Fusiformis*-like microörganisms adherent by their full length. These are never consistently present on *Foaina.* On some specimens of *F. delicata* a few of the short rods, *"Fusiformis hilli,"* occur. These, however, are not the same as the microörganisms on *Devescovina.* They more commonly occur on some specimens of *Foaina hilli,* but their abundance and distribution vary, and they are present also in the lumen of the gut, free of contact with the flagellates (Kirby, 1938*b*).

Adherent spirochaetes are absent from most species, but they are present on some. They do not form a dense cilia-like covering in any species except *F. hilli.* Usually, when present, they are in groups on the anterior or posterior end, or both (fig. E, 10); only rarely, as in some specimens of *F. appendicula* and in *F. hilli,* are they present on the whole surface. The spirochaetes are relatively long, often measuring 8–10μ. There is some variability in their abundance, or even in their occurrence, on different flagellates of the species in an infection, or in different colonies or host species, but the characteristic is constant enough to be useful in identification. Some species never have spirochaetes; and *F. hamata,* for example, is always, in all its hosts, provided with a group of spirochaetes on the posterior end.

### KEY TO THE SPECIES OF FOAINA

In using this key for identification of species it must be kept in mind that the characteristics given apply only to the fully developed, average-type specimens. There may be very close resemblances between certain forms of different species. The following descriptive section, together with the diagnoses, will be more useful than the key. A key, however, has the merit of pointing out certain salient characteristics to which further consideration can be given.

| | | |
|---|---|---|
| 1. | Parabasal body simple, with no branching | 2 |
| | Parabasal body typically with one or more rami | 20 |
| 2. | Average length of cresta less than 7μ | 3 |
| | Average length of cresta more than 7μ | 10 |
| 3. | Trailing flagellum very slender | 4 |
| | Trailing flagellum a stouter cord | 6 |
| 4. | Length of cresta 3μ or less | 5 |
| | Length of cresta 5μ or more | *F. humilis* |
| 5. | Trailing flagellum very slender | *F. parvula* |
| | Trailing flagellum stout | *F. grassii* |
| 6. | Average body length 17μ or less | 7 |
| | Average body length 24μ | *F. gracilis* |
| 7. | Cusp of axostyle not enlarged | 8 |
| | Cusp of axostyle often prominently enlarged | 9 |
| 8. | Not exceeding 20μ in length, with cresta 8–9μ in larger specimens | *F. ovata* |
| | Often exceeding 20μ in length, cresta usually less than 6μ in largest specimens | *F. exempta* |
| 9. | Average cresta length less than 5μ; parabasal short | *F. solita* |
| | Average cresta length more than 5μ; parabasal longer, curved around nucleus | *F. minuscula* |

10. Cresta usually, or often, reaching to or rounding posterior end of the body........ 11
    Cresta only occasionally reaching to the posterior end of the body................ 12
11. Trailing flagellum very slender.......................................... *F. dogieli*
    Trailing flagellum moderately stout.......................................... *F. costata*
12. Parabasal apparatus with long free filament typically passing posteriorly for some distance at periphery of body.......................................... *F. nana*
    Free parabasal filament not so long.......................................... 13
13. Trailing flagellum markedly band-formed.......................... *F. taeniola*
    Trailing flagellum cordlike.......................................... 14
14. Parabasal body formed like the lower part of an E, including the center bar; transverse part across the posterior part of the nucleus, short free filament extended toward margin .......................................... 15
    Parabasal body otherwise formed.......................................... 18
15. Nucleus with one to several peripheral nucleoli and a relatively large, deep-staining body composed of 5 or 6 granules.......................................... *F. signata*
    Nucleus typical, without this deep-staining body.......................................... 16
16. Cresta typically 12–17μ in length.......................................... *F. acontophora*
    Cresta 12μ or less in length.......................................... 17
17. Cusp of axostyle usually markedly enlarged.......................................... *F. hamata*
    Cusp of axostyle not enlarged.......................................... *F. delicata*
18. After short transverse part near posterior level of nucleus, parabasal body turned forward in a loop often to the anterior level of the nucleus, then passing transversely at this level.......................................... *F. reflexa*
    Parabasal without this sharp U-formed bend, often sigmoid in form............. 19
19. Nucleus much elongated transversely and often curved; trailing flagellum stout *F. funifera*
    Nucleus ellipsoidal and not curved; trailing flagellum not so stout......... *F. falcifera*
20. Average length less than 25μ; ramus of parabasal single and undivided.......... 21
    Average length more than 30μ; rami of parabasal often more than one........... 22
21. Ramus of parabasal short; arising at the angle of the longitudinal and transverse part of the main substance, and in line with the latter part................ *F. duo*
    Ramus of parabasal longer, curved, not in line with transverse part...... *F. appendicula*
22. Two rami of parabasal often present, so arranged as to form, with the longitudinal and transverse parts of the main parabasal, a cross...................... *F. hilli*
    Parabasal rami often more than two, not forming a cross...................... 23
23. Parabasal typically with 1–7 short rami attached at the bend of the main body; nucleus markedly curved in its longer diameter.................... *F. nucleoflexa*
    Parabasal typically with a long, barlike outgrowth from which arise 1, 2, or 3 branches; nucleus ellipsoidal.......................................... *F. ramulosa*
    Parabasal usually with 1–5 rami at intervals along the main part, the first often close to the blepharoplast.......................................... *F. pectinata*

## COMPARISON OF SPECIES OF FOAINA

The smaller and simpler animals are, the greater is the difficulty in establishing morphological distinctions between congeneric species. The simplest of all flagellates in termites, *Tricercomitus,* has only one species, so far as can be determined by microscopic observation, in more than a hundred members of *Kalotermes* sensu lato. The difficulties of satisfactory classification are considerable when we must take into account the variability of the characteristics of *Foaina* that can be used for taxonomic purposes, such as the thickness of the trailing flagellum, the length of the cresta, the enlargement of the cusp of the axostyle, and the form of the parabasal body. One must decide when to recognize differences in these characteristics as sufficient to distinguish species.

Even when, as in the present instance, such decisions are based on study of a large amount of comparative material, the facts are subject to different interpretations. The species distinctions made here, however, were arrived at only after prolonged study and repeated checking; and each point of distinction has been based on actual comparison of many specimens.

Nine of the twenty-five species studied by me can be recognized easily, with no likelihood of uncertainty so far as distinction from other described species is concerned. These are:

*F. dogieli* (fig. B, 1, 2), by its relatively very slender trailing flagellum, together with the very long cresta, which often reaches to the posterior end of the body.

*F. taeniola,* by its ribbon-formed trailing flagellum (fig. A, 7).

*F. signata* (fig. B, 7) by its unique nuclear structure (pl. 26, fig. 36).

*F. appendicula* (fig. C, 2), *F. duo* (fig. C, 3), *F. hilli* (fig. C, 4), *F. nucleoflexa* (fig. C, 5), *F. pectinata* (fig. C, 7), and *F. ramulosa* (pl. 30, fig. 65; fig. C, 6), which all have outgrowths of the parabasal body, by the form, number, and arrangement of these outgrowths, as has been indicated in the key.

The smallest and simplest species are *Foaina parvula* (fig. A, 3), *F. grassii* (fig. A, 1), and *F. solita* (fig. A, 2). All these have crestas usually less than 5μ in length, a small ovoidal or bacilliform parabasal body, and a body size usually averaging about 11 or 12μ × 5 or 6μ. Body size larger than usual is sometimes come upon, and, if there is agreement in other respects, the forms are not to be separated for this reason. That is the situation in *F. solita* in *Rugitermes kirbyi* and *R. panamae* (p. 183). In *F. parvula* the trailing flagellum is always very slender (pl. 23, fig. 10); in the other two species it is a moderately stout cord (pl. 23, figs. 2, 4). There are obvious distinctions between the last two species, as will be noted in the account of *F. solita* (p. 184). The most positive difference is in the cresta, which is shorter in *F. grassii* and is often difficult to recognize, whereas such a difficulty never arises in *F. solita.*

There is also a comparatively small body size and a short cresta in *F. humilis* (fig. A, 4), *F. excmpta* (fig. A, 5), and *F. minuscula* (fig. B, 4); in these the average body length is about 14–17μ, the width about 6–8μ, the crestas 3–7μ. Relatively very large forms occur, however, in *F. exempta. F. ovata* (fig. A, 6) is smaller, and its cresta a little longer. In these species the parabasal body curves around part of the nucleus, against the membrane; it may have a C form, or be extended transversely across and beyond the nucleus, and there may be a short free filament at the end.

*Foaina exempta* has a shorter cresta, on the average, than the other species in this second group; there is no enlarged cusp, which distinguishes it further from *F. solita* and *F. minuscula;* the trailing flagellum is stouter than in *F. humilis* and *F. parvula,* but slenderer than in *F. grassii* and *F. solita.* The flagellate averages larger, and develops very much larger forms than *F. ovata,* which, furthermore, has a good deal longer cresta in specimens of the same size.

*Foaina minuscula* has a prominent cusp (fig. B, 4) which is so constant as to constitute a conspicuous difference from *F. excmpta* and *F. ovata,* in both of which no enlarged cusp has been observed (fig. A, 5, 6). Spirochaetes, not present on the other three species, are adherent to the posterior end of *F. minuscula.* The trailing flagellum is much stouter than that of *F. humilis,* which sometimes has an enlarged cusp.

*Foaina ovata* (fig. A, 6), which is usually smaller than the other species under consideration in this group, differs from the first group of species (*F. grassii, solita, parvula*) in its longer cresta (4–9μ). This cresta is slender and in the majority of specimens is difficult to distinguish from the base of the trailing flagellum, a difficulty not encountered in *F. humilis.* The trailing flagellum, though not stout, is not so slender as that of *F. humilis.* In the material examined *F. humilis* frequently showed a somewhat enlarged cusp and rings around the posterior part of the axostyle, neither of which was seen in *F. ovata.* The parabasal body in larger specimens of *ovata* often extends some distance beyond the nucleus, and has a short free filament. The parabasal body of *F. humilis* does not extend so far beyond the nucleus.

*Foaina gracilis* (fig. A, 9) is a much larger species than any mentioned so far in this comparison; it differs also in the form of the parabasal body, which almost completely surrounds the nucleus and does not extend free of the membrane. It differs from all species yet to be considered in the very short cresta, measuring only 3–5μ, which is like that of the very much smaller *Foaina solita.*

*F. nana* (fig. A, 10) and *F. costata* (fig. A, 11) can be recognized by the long free parabasal filament, which often extends posteriorly for some distance at the periphery of the body. The latter species is, on the average, considerably larger than the former; and some specimens exceed in size any that occur in *F. nana.* The cresta is much longer, its minimum length coming only a little short of the maximum of that of *F. nana.* The breadth of the cresta of *F. costata,* as seen in tangential view, is comparatively great (pl. 25, figs. 28, 29). *F. costata* is rather like an enlarged form of *F. nana;* but the differences between them are too great to permit of their classification as the same species.

A group of species of moderate or large size, of which *F. hamata* (fig. B, 3) may be regarded as typical, has the parabasal body curved around the nuclear membrane, often with two sharp bends, one near the blepharoplast and one at the beginning of the transverse part. The transverse part usually remains at the posterior level of the nucleus, and the main substance does not extend far beyond it. There is a free parabasal filament, reaching to the periphery and sometimes turned a short distance posteriorly, but not long like that of *F. nana.* This group includes *F. hamata, F. delicata* (fig. B, 5), *F. acontophora* (fig. B, 6), and *F. signata* (fig. B, 7). *F. minuscula* (fig. B, 4), which has been considered before, has a similar parabasal body and is related to this group also, as it resembles the smallest individuals of *F. hamata.*

Excluding *F. minuscula,* the smallest species in this group is *F. delicata.* The type of nucleus readily distinguishes that species from *F. signata; F. acontophora* differs from *F. delicata* in the usually much longer cresta and in the frequent curvature of the nucleus; *F. hamata* differs from the latter species in the usual marked enlargement of the cusp, which was never seen to be enlarged in *F. delicata,* and in the development of much larger forms. An aid in differentiating between *F. delicata* and *F. hamata,* in the material studied, is the presence of a tuft of spirochaetes on the posterior end of the latter, and its absence from the former. *Foaina acontophora* differs from *F. hamata* in the slenderer and usually much longer cresta. The relationship between these two species is further discussed in the account of *F. acontophora* (p. 200). *F. signata* has very little or no enlargement of the cusp, and in this, as well as in its unique nuclear characteristic, it differs from *F. hamata.* The rings on the surface (pl. 27, figs. 37, 38), furthermore, have been seen on no other devescovinid.

The three remaining species, *F. falcifera* (fig. B, 8, 9), *F. funifera* (fig. B, 10), and *F. reflexa* (fig. C, 1), have parabasal bodies typically shaped differently from those of the *hamata* group. *F. reflexa* can be distinguished from the others by the sharp bend anteriorly, in typical specimens, of the part of the parabasal beyond the second turn, bringing the distal part of the parabasal near the anterior level of the nucleus. In many specimens it extends posteriorly from this position in a band form. In *F. funifera* the terminal part of the parabasal is often brought anteriorly also, but not by the sharp bend of *F. reflexa.* Also, the nucleus of the former species is transversely elongated to a much greater degree, and its trailing flagellum is often stouter than in the latter species. In *F. falcifera,* in larger individuals, the parabasal body continues transversely beyond the nucleus as a stout structure, though the first part may be shaped much as in *F. hamata.* There is often a close similarity to *F. funifera* in this structure, but the nucleus of *F. falcifera* is ellipsoidal and not curved, and the trailing flagellum is much more slender.

The species of *Foaina* described by Grassé (1938) as *Parajoenia decipiens* has been omitted from both the above comparison and the key, since the description is insufficiently accurate to be included. It is discussed below (p. 210).

## MORPHOLOGY AND DIAGNOSIS OF SPECIES OF FOAINA

### **Foaina grassii** (Duboscq and Grassé) comb. nov.

Plate 23, figures 1–3; figure A, 1

*Monocercomonas termitis,* partim, Comes, 1914, Boll. Accad. Gioenia Sci. Nat. Catania, (2) fasc. 33:15; non *Monocercomonas termitis* Grassi = *Hexamastix termitis.*

*Janickiella grassii* Duboscq and Grassé, 1923, C. r. Acad. Sci., 177:178.

*Janickiella grassii* (stade *Eutrichomastix*) Duboscq and Grassé, 1924, C. r. Soc. Biol., 90:1444, figs. 6–8.

*Type host.*—*Kalotermes flavicollis* (Fabricius). Europe. T-323 (Emerson). (Xenosyntype slide TP-197:2.)

*Diagnosis.*—(After Duboscq and Grassé): length without projecting axostyle 10–12$\mu$, including projecting axostyle up to 20$\mu$; three anterior flagella 20$\mu$ long; stout trailing flagellum about 50$\mu$ long; large blepharoplast; very short costule; parabasal body more or less pyriform, applied to nucleus; axostyle very long, slender, surrounded at its base by a spiral of mitochondrial granules; frontal granules present in region anterior to nucleus; nucleus more or less spherical; ingests bacteria and wood. (Original): length 11 (8–19)$\mu$; width 5 (3.5–10.5)$\mu$; anterior flagella about 15$\mu$ long; trailing flagellum a moderately stout cord, often 35–40$\mu$ long; cresta small, narrow, length 1.5–3$\mu$; parabasal body bacilliform or more or less ovoidal, usually shorter than nucleus, no free filament; posterior part of

**axostyle not enlarged, trunk projecting often 1–8μ; nucleus 1.2–2 × 0.7–1.5μ and 2.5–4.5 × 2.3μ (see below); no adherent microörganisms.**

In 1923 Duboscq and Grassé published an account of the small flagellates of *Kalotermes flavicollis,* in which they recognized three distinct species, *Hexamastix termitis, Trichomonas dogieli,* and *Janickiella grassii.* They also mentioned *Trimitus* sp., which at that time they believed to be a stage of *Janickiella,* but later (1934) regarded as a separate species. In a note published in 1924 they grouped the flagellates earlier designated as *Trimitus, Janickiella,* and *Trichomonas* into the life cycle of *Janickiella grassii.* I will later (p. 197) give reasons for transferring the species named *Trichomonas dogieli* to the genus *Foaina* as *F. dogieli.*

I have been able to study specimens of *Foaina grassii* through Professor A. E. Emerson, who gave me a few living *Kalotermes flavicollis* which he brought from Europe. My observations are essentially in agreement with those reported by the French investigators.

In living material, *Foaina grassii* was noted as a small, active flagellate, moving in a jerky manner, and present in abundance. The three anterior flagella usually are united into a bundle moving as a unit; and the long trailing flagellum is moderately stout, tapered to a filament in its posterior third, and adherent to the body in its anterior portion.

The axostyle is obscure at best, but the trunk does not taper so much within the cytoplasm as is shown by Duboscq and Grassé (1924). (Drawings that are more correct in this respect were published by them in 1933—their text figs. VIII, c; LII; LXIX.) The short terminal tapering portion seems to be free of a cytoplasmic sheath, but when, as sometimes happens, the body has receded from the posterior part of the trunk, there is cytoplasm around this.

In osmic vapor-fixed, Heidenhain haemotoxylin-stained material (pl. 23, figs. 1, 2) the parabasal body appeared homogeneous black, but more abundant material might have disclosed the two parts described by Duboscq and Grassé (1924). The parabasal body could also be seen in Bouin-fixed Heidenhain material (pl. 23, fig. 3) and Schaudinn-Delafield material, though in the former it was very little stained.

The blepharoplast appears to be a single large granule. In the posterior cytoplasm there usually are numerous rather large granules, which stain with iron-haematoxylin after osmic vapor, Bouin's, or Schaudinn's fixation. In some specimens, but by no means in all, these are especially concentrated around the axostyle just posterior to the nucleus. Capitular granules are present in the papilla, but these are not so abundant as those in *F. dogieli.* A clear area along the anterior border of the papilla, extending to the nucleus, is visible in many specimens (fig. A, 1), but is less conspicuous than in some other species of *Foaina.*

The cresta (pl. 23, fig. 2) is small, yet it is considerably larger than Duboscq and Grassé represented it to be (1924, fig. 7). It is flattened and subtriangular in shape, with the longest side peripheral. The trailing flagellum is very slender where it passes along the edge of the cresta to meet the blepharoplast. In most prepared material the cresta cannot be seen as separate from the

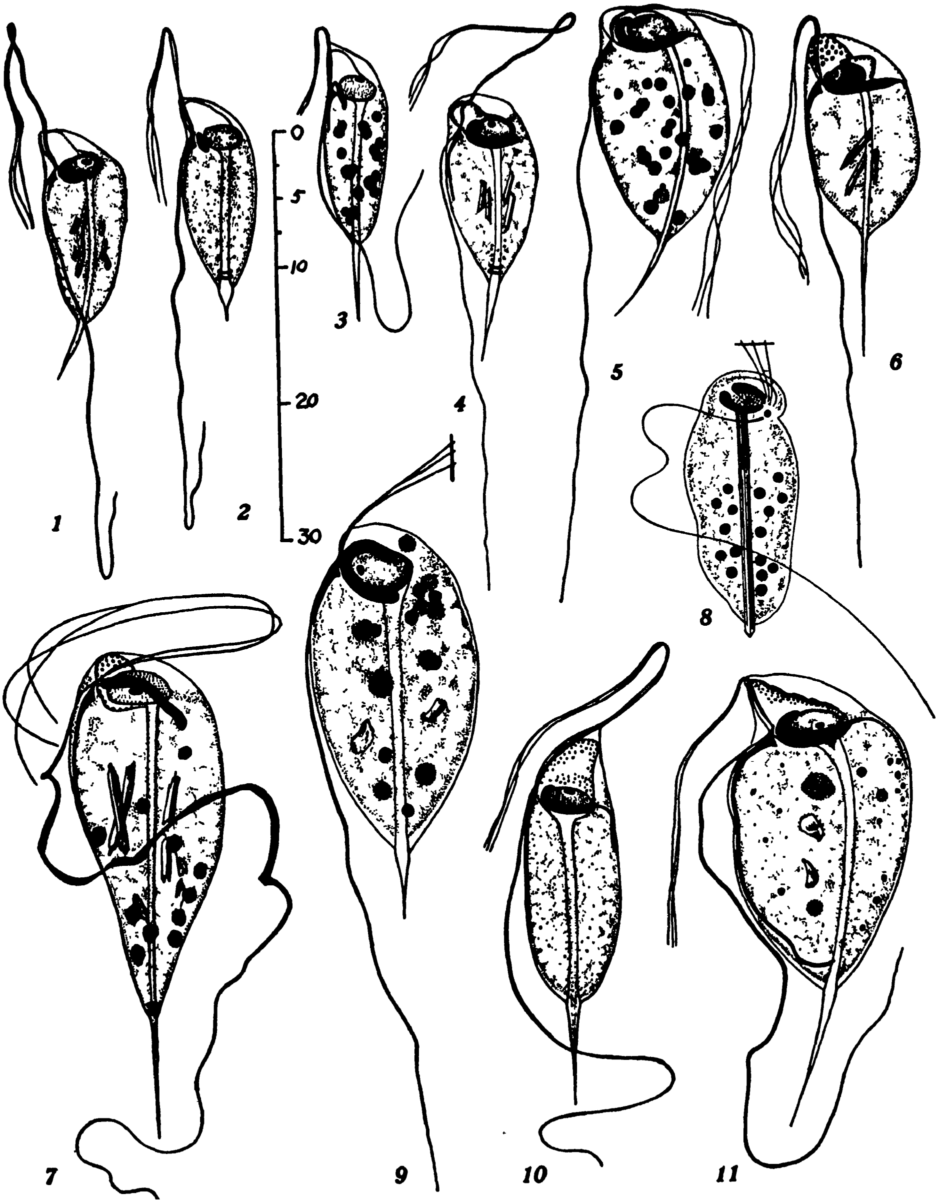

Fig. A. Species of *Foaina*. 1. *Foaina grassii* (Duboscq and Grassé) comb. nov. from *Kalotermes flavicollis*, Europe. 2. *F. solita* sp. nov. from *Cryptotermes dudleyi*, Panama. 3. *F. parvula* sp. nov. from *Neotermes* sp. T-2012, Tanganyika. 4. *F. humilis* sp. nov. from *Cryptotermes brevis*, Mexico. 5. *F. exempta* sp. nov. from *Neotermes insularis*, Australia. 6. *F. ovata* sp. nov. from *Neotermes howa* var. *mauritiana*, Mauritius. 7. *F. taeniola* sp. nov. from *Paraneotermes simplicicornis*, California. 8. *F. gracilis Janicki* from *Neotermes connexus*, Hawaii (after Janicki, 1915). 9. *F. gracilis* Janicki (original). 10. *F. nana* Kirby from *Cryptotermes dudleyi*, Tanganyika. 11. *F. costata* sp. nov. from *Neotermes insularis*, Australia. 8, × 1000; others and scale, × 1750.

proximal part of the trailing flagellum, which then appears as thick as in its middle portion.

The nucleus appeared considerably larger in certain material fixed in osmic vapor (pl. 23, fig. 2) than in Bouin-fixed material (pl. 23, fig. 3). The larger measurements recorded above were made from the former preparations.

As was noted by Duboscq and Grassé (1924), Comes (1914) was concerned in part with this flagellate in his account of what he thought to be *Monocercomonas termitis.* Some of his figures evidently represent *F. grassii;* others, *F. dogieli.* He stated that he had found it both in *"Termes" flavicollis* and *"Termes" lucifugus,* but made his studies mainly on flagellates from the former host. The latter record must have been made from an actual observation of *Hexamastix termitis.* The reproductive processes are said to include fission, conjugation with reduction, formation of secondary nuclei, and rosette formation. He mistook the iron-haematoxylin-staining cytoplasmic granules for secondary nuclei.

The rosettes, which Duboscq and Grassé included in the cycle of *Janickiella grassii* as representing the end of schizogony, were probably agglomerations of *Tricercomitus,* with no relation to schizogony. I have observed such a grouping of *Tricercomitus* in living material from *Kalotermes flavicollis,* and previously described the phenomenon in *Kalotermes hubbardi* and *Cryptotermes dudleyi* (1930, p. 406); Grassé himself (1926) described similar agglomeration in *Proteromonas,* attributing it to the influence of the medium.

### **Foaina solita** sp. nov.

Plate 23, figures 4–9; figure A, 2

*Type host.—Cryptotermes dudleyi* Banks. Panama.
T-239. Balboa. (Syntype slides TP-168:8, 5; 163:6.)
T-1013. Tanga, Tanganyika Territory. (Homosyntype slide TP-1024:19.)

*Additional hosts*
*Cryptotermes longicollis* (Banks). Panama.
T-223, 225. Taboga Island. (Homosyntype slides TP-137:31; 142:13.)
*Cryptotermes queenslandis* Hill.
T-519. (Hill 3492.) S.W. Australia. (Homosyntype slide TP-519:21.)
*Cryptotermes* sp. nov. Madagascar, Mauritius.
T-4506. Tamatave. (Homosyntype slide TP-3190:1.)
T-4525. Reduit, Mauritius.
*Cryptotermes* sp. Madagascar.
T-4375. Near Mahabo. (Homosyntype slide TP-3138:5.)
*Kalotermes* (s. lat.) sp. Portuguese India. (*"Coptotermes heimi."*)
T-317. (De Mello.) Damaum. (Homosyntype slide TP-323:1.)
*Glyptotermes angustus* Snyder. Panama.
T-127. Barro Colorado. (Homosyntype slides TP-66:6; TP-64:3, 6.)
*Glyptotermes dilatatus* Bugnion and Popoff. Ceylon.
T-318. (Cleveland. Collier.) (Homosyntype slide TP-263:7.)
*Glyptotermes parvulus* Sjöstedt. Gold Coast.
T-301. (Silvestri.) (Homosyntype slides TP-318:1, 2.)
*Glyptotermes tuberculatus* (Froggatt). Australia.
T-4608. (Cleveland-Hill.) A. C. T. (Homosyntype slide TP-3284:52.)

*Glyptotermes* sp. nov. Uganda.
T-2072. Near Kampala. (Homosyntype slides TP-2023:27, 23.)
*Glyptotermes* sp. nov. Belgian Congo.
T-3018. Near Rutshuru. (Homosyntype slide TP-2034:8.)
*Glyptotermes* sp. nov. Ruanda-Urundi.
T-3022. Kakitumba. (Homosyntype slide TP-2037:12.)
*Kalotermes jeannelanus* Sjöstedt. East Africa.
T-1092. Taveta, Kenya Colony. (Homosyntype slide TP-1077:11.)
T-2013. Mount Meru, Tanganyika T. (Homosyntype slide TP-1088:8.)
T-2088. Hoima, Uganda. (Homosyntype slide TP-2027:4.)
*Kalotermes repandus* Hill. Fiji Islands.
T-516. (Hill 4064.) (Homosyntype slide TP-516:4.)
*Kalotermes* sp. Madagascar.
T-4341. Near Maevatanana. (Homosyntype slide TP-3110:9.)
*Neotermes castaneus* Burmeister. Florida.
T-530. Pine Crest. (Homosyntype slide TP-533:24.)
*Neotermes connexus* Snyder. Hawaii.
T-305. (Bryant.) (Homosyntype slide TP-198:36.)
*Neotermes greeni* Holmgren. Ceylon.
T-310. (Cleveland. Collier.) (Homosyntype slide TP-253:109.)
*Neotermes holmgreni* Banks. Panama.
T-222. Taboga Island. (Homosyntype slides TP-134:19; 132:10.)
*Neotermes sonneratiae* Kemner. Java.
T-4574. Angke. (Homosyntype slide TP-3258:7.)
*Neotermes tectonae* Dammerman. Java.
T-4542. Telawa. (Homosyntype slide TP-3227:8.)
*Procryptotermes* sp. nov. Reunion.
T-4516. Pointe des Galets. (Homosyntype slide TP-3198:5.)
*Rugitermes kirbyi* Snyder. Costa Rica.
T-135. Cartago. (Homosyntype slide TP-76:20.)
T-148. Cartago. (Homosyntype slide TP-92:18.)
*Rugitermes panamae* Snyder. Panama.
T-191. Barro Colorado. (Homosyntype slide TP-111:13.)
T-120. Barro Colorado. (Homosyntype slide TP-56:5.)

*Diagnosis.*—(From type host): length 11.1 (7.6–17.7)μ; width 5.6 (3.2–9.2)μ; anterior flagella about 20μ long; trailing flagellum a moderately stout cord, 35–50μ long; cresta narrow, length 3.7 (3–4.5)μ; parabasal body bacilliform, equal, or nearly equal, to nucleus in length, restricted to dorsal side, capitular granules few or none; trunk of axostyle moderately stout, with or without an enlarged, rounded cusp, 2–4 rings surrounding trunk just before projection, length of projection often about 2μ; nucleus rounded, 2–3 × 1.5–2.5μ; no adherent microörganisms. (From *Rugitermes kirbyi*): length, including projecting axostyle, 19.2 (12.5–25.4)μ; width 5.4 (3.9–6.8)μ; projecting axostyle about 2.5μ; cresta 4.7 (3.1–5.4)μ. (From *Neotermes connexus*): length 10.5 (7.5–15.5)μ; width 5.5 (3–9)μ. (From *Glyptotermes parvulus*): trailing flagellum more slender than in type; cresta length often about 2.5μ; parabasal body bacilliform, maximum length equaling that of nucleus; axostyle with enlarged projecting cusp and rings; nucleus 2–3.5 × 1–1.7μ. (From *Glyptotermes* sp. nov. T-2072): length 10.7 (6.6–19)μ; width 4.7 (3.3–8.3)μ; cresta 3 (2.5–4.2)μ.

In many of its hosts, *Foaina solita* is associated with *F. nana,* as it is in the type host. There are, however, marked differences between the two species. In some hosts *F. solita* occurs alone or with a species of *Foaina* not *F. nana;* and *F. nana* occurs in some hosts without *F. solita.*

As recorded above, the average length of specimens from *Rugitermes kirbyi* is considerably greater than that of specimens from *Cryptotermes dudleyi.*

There were in both *R. kirbyi* and *R. panamae* many much larger specimens than in other hosts, but otherwise they agreed with the type in all structural characters.

The trailing flagellum in specimens from the type host is relatively stout, and reaches a length 2–5 times that of the body (pl. 23, fig. 5). The blepharoplast, as shown in material fixed in osmic, is a relatively large spheroidal body. In the type material from *Cryptotermes dudleyi,* suitably prepared for their demonstration, the rings around the posterior part of the trunk of the axostyle were conspicuous (pl. 23, fig. 4). On the same slides rings were not observed in *Foaina nana.* Usually there are two of these. They appeared only in sufficiently heavily stained iron-haematoxylin preparations, and were not recognizable at all in some material of *Foaina solita.* On slides from *Rugitermes kirbyi* the two rings appeared slender (pl. 23, fig. 6), and were usually recognizable, seen in optical section, only as apparent granules beside the trunk of axostyle. One of them is situated near the place where the projection from the cytoplasm begins, the other a short distance anterior to this.

A characteristic of *Foaina solita* is the usual absence of a conspicuous clear area anterior to the nucleus—the "cytostome"-like area whose presence is a prominent feature of *F. nana.* There may be a narrow clear area along the anteroventral margin of the capitulum (pl. 23, fig. 4), but it is never so broad as in some species of the genus.

The presence of an enlarged cusp of the axostyle is a variable characteristic. In preparations from certain hosts most specimens have such a cusp, but some do not. This was true in the type host. In the flagellate in other termites an enlarged cusp may be present, or not. In some hosts (*Kalotermes jeannelanus, Neotermes erythraeus, Glyptotermes* T-2072, and *Glyptotermes tuberculatus*) it was not observed in any specimens.

There is some similarity between *F. solita* and *F. grassii,* but the two species are undoubtedly different. The cresta is smaller in *F. grassii,* and it is usually difficult to distinguish it from the base of the trailing flagellum. This may easily be done in all suitably stained specimens of *F. solita.* The parabasal body is considerably narrower than that of *F. grassii,* as observed in my preparations made by the same technique. It does, however, resemble the parabasal figured in that species by Duboscq and Grassé (1924). There is no enlarged cusp in *F. grassii,* whereas that is a frequent characteristic of *F. solita.*

As will be noted in the list of hosts given above, *F. solita* has been found, along with *F. gracilis* and *F. nana,* in *Neotermes connexus* of Hawaii, the species studied by Janicki under the name *Neotermes castaneus.* Janicki (1915) mentioned two small flagellates from this termite of Hawaii. Form I, about 9μ in diameter, he found somewhat abundant. Form I is the *Monocercomonoides* type of flagellate, which I have seen in a number of Kalotermitinae. It has been observed in both living and fixed preparations of *Neotermes connexus.* Form II, which averaged about half the size of the other, he seldom encountered. He stated that there is an extraordinarily long trailing flagellum, possibly several delicate anterior flagella, and an elongated parabasal body. He did not find an axostyle, but stated that the presence of this is not excluded. As calculated from the magnifications given, the larger forms drawn were about 7μ in diameter, the smaller ones, 5μ. Since *Foaina solita* and *F. nana* are both usually common in *Neotermes connexus,* though not abundant in all preparations, it is most likely that Janicki described small *Foaina* forms (pl. 18, figs. 71, 72) as form II. His figures showing division in smaller specimens (fig. 73) may represent *Tricercomitus divergens,* which has been recorded from *Neotermes connexus* (Kirby, 1930), and which in size and structure during division (Kirby, 1930, pl. 44, figs. 20–23) is much like the specimens figured by Janicki.

### **Foaina parvula** sp. nov.

Plate 23, figure 10; figure A, 3

*Type host.*—*Glyptotermes contracticornis* (Snyder). Costa Rica.
T-146. Cartago. (Syntype slides TP-87:9, 6.)

*Additional hosts*
*Cryptotermes* sp. nov. Madagascar.
T-4403. Near Tulear. (Homosyntype slide TP-3151:10.)
*Glyptotermes montanus* Kemner. Java.
T-324. (Cleveland. Collier.) (Homosyntype slide TP-262:12.)
*Glyptotermes neotuberculatus* Hill. Australia.
T-513. (Hill 3194.) Aust. Cap. Ter. (Homosyntype slide TP-513:5.)
*Glyptotermes taveuniensis* Hill. Fiji Islands.
T-515. (Hill 4065.) (Homosyntype slide TP-515:39.)
*Kalotermes* (s. str.) sp. nov. Tanganyika Territory.
T-3025. Eastern edge of Serengeti Plains. (Homosyntype slide TP-2044:12.)
*Neotermes castaneiceps* Sjöstedt. Madagascar.
T-4505. Tamatave. (Homosyntype slide TP-3205:9.)
*Neotermes erythraeus* Silvestri. Eritrea.
T-312. (Silvestri.) (Homosyntype slides TP-321:1, 2.)
*Neotermes longus* (Holmgren.) Madagascar.
T-4484. Perinet. (Homosyntype slide TP-3184:10.)
*Neotermes* sp. Tanganyika Territory.
T-2012. Mount Meru. (Homosyntype slide TP-1085:3.)
*Neotermes* sp. nov. Madagascar.
T-4468. Near Ambovombe. (Homosyntype slide TP-3171:4.)
*Kalotermes* (s. lat.) sp. Transvaal.
T-4240. Near Nylstroom. (Homosyntype slide TP-3069:13.)

*Diagnosis.*—(From type host): length 12.5 (8–18)μ; width 4.3 (3–6)μ; trailing flagellum very slender; cresta length 2.5 (1.5–3)μ; parabasal body bacilliform, equal or nearly equal to the nucleus in length; capitular granules few or none; trunk of axostyle usually with little or no enlargement at the posterior end of the body, rings present but inconspicuous; nucleus similar to that of *F. solita;* no adherent microörganisms.

The size of the trailing flagellum makes it necessary to distinguish this flagellate as a separate species from *F. solita,* which it otherwise closely resembles. The distinction is very marked in this respect between the type of *F. solita* and the type of *F. parvula.* In infections of different hosts, the stoutness of this flagellum may not exactly agree with the type; yet the difference is insufficient for separation of species. When the variations of the species *solita* and *parvula* approach one another, identification is necessarily uncertain. For example, the trailing flagellum of the flagellate from *Glyptotermes* T-2072 of Uganda is not so very much stouter than that of *Kalotermes* T-4240 of the Transvaal. Identification of the former as *F. solita* and the latter as *F. parvula* is much less certain than when the two types are concerned. There is also some difficulty in identification of the flagellate in *Neotermes erythraeus,* which has a stouter trailing flagellum than is usual for *F. parvula.* In the stoutness of the trailing flagellum, in fact, there is a series in which the drawing of species limits is somewhat arbitrary. There is, however, no doubt of the validity of the two species recognized here; but, if other characteristics than those the microscopical study of these small flagellates affords could be considered, it is possible that there would be more than two species.

*Foaina parvula* belongs to the group of species with few if any wood particles in the cytoplasm, and more or less abundant iron-haematoxylin-staining spherules (fig. A, 3). The difference from such species as *F. nana* in this feature of the cytoplasm is striking. Both *F. parvula* and *F. nana* occur in *Glyptotermes taveuniensis.* A large proportion of the former species have the spherules, and the cytoplasm appears rather dense and granular. There are few or no wood particles. In *F. nana* there are many small wood particles, and the cytoplasm appears more vacuolated. The two species can often be readily separated by the cytoplasmic characteristics.

### **Foaina humilis** sp. nov.

Plate 24, figures 11–12; figure A, 4

*Type host.—Cryptotermes brevis* Walker.
T-261. Colima, Mexico. (Light 75 Me.) (Syntype slides TP-219:32, 17.)
T-240. Puerto Rico. (Xenosyntype slide TP-155:11.)
T-4600. Lima, Peru. (Xenosyntype slide TP-3283:4.)
T-4011. Durban, South Africa. (Homosyntype slide TP-2072:18.)

*Additional hosts*
*Cryptotermes grassii* Silvestri, *nomen nudum.* Iquique, Chile.
T-320. (Silvestri.) (Homosyntype slide TP-325:1.)
*Cryptotermes piceatus* Snyder. Hawaii.
T-321. (Fulloway.) (Homosyntype slides TP-207:2, 9.)

*Diagnosis.*—(From type host T-261): length 13.6 (7–19)μ; width 6.9 (3.5–10)μ; trailing flagellum slender; cresta length 6 (5–7)μ; parabasal body bacilliform, or curved in C form around part of nucleus; capitular granules abundant; trunk of axostyle with projection often 4–10μ, expanded cusp or not, usually not in type material, continued in long filament; nucleus 2.4 (1.7–3.3) × 1.5 (0.8–1.7)μ; no adherent microörganisms. (From type host T-240): length 16 (12.5–21)μ; width 7.5 (5–10.5)μ; cresta length 6 (5.2–6.5)μ; projection of axostyle often 4–6μ; nucleus 3.3 (2.6–4.4) × 2.2 (1.7–2.6)μ. (From *Cryptotermes* T-4011): length 8 (6–12)μ; width 4.5 (3–7)μ; cresta 5.6 (4.5–7)μ.

There is only one species of *Foaina* in *Cryptotermes brevis* and the other hosts listed above.

As noted above, the body size averages considerably less in the specimens from the South African *Cryptotermes* than in the others recorded. In *Cryptotermes brevis* from Mexico and Peru, however, there were some specimens as small as those in the South African termite; and the flagellates agree in length of cresta and in trailing flagellum. The size difference does not warrant specific distinction.

Slender trailing flagella occur also in *Foaina parvula* and *F. dogieli. F. humilis* can readily be distinguished from those species by the cresta, which is considerably longer than that of the former and considerably shorter than that of the latter. In small specimens of *F. humilis* the cresta may reach the posterior end of the body.

The numerous capitular granules were particularly evident in the material from the Puerto Rico *Cryptotermes brevis* (pl. 24, fig. 12). These slides had been counterstained with eosin. On them, also, numerous similar granules were demonstrated along the trunk of the axostyle of *F. humilis.* They were seen also, less clearly, in material from the Mexican termite. The eosin counterstain seems to be favorable for demonstrating these granules.

The trunk of the axostyle always projects from the posterior end of the cytoplasm. The length of this projection varies from very little up to more than the length of the body itself. In most of the specimens there was no marked enlargement, but some specimens on all slides, and the majority of those in the material from Peru, had a prominent enlarged cusp. In some of the last, indeed, the cusp was relatively enormous in size. The projection ends in a relatively long filament.

Rings or bands around the posterior part of the runk of the axostyle are well defined in all my iron-haematoxylin-stained preparations.

### **Foaina exempta** sp. nov.

Plate 24, figure 13; figure A, 5

*Type host.*—*Neotermes insularis* White. Australia.
T-308. (Cleveland.) (Syntype slide TP-320:210.)

*Diagnosis.*—Length 17 (8–39)μ; width 8 (4.5–16)μ; trailing flagellum a moderate-sized cord; cresta 4 (3–6)μ; parabasal body in smaller individuals bacilliform, in larger ones elongated, turned transversely across nucleus, with a sharp bend at the blepharoplast and a rather long limb on the opposite side of the blepharoplast from most of the structure; capitular granules few or none; axostyle projecting several microns, but without posterior enlargement; nucleus with a number of peripheral, deep-staining nucleolar granules, size 3.5 (1.7–4.5) × 2.7 (1–3.5)μ; cytoplasm dense-appearing, with no quantity of wood, containing numerous deep-staining spherules; no adherent microörganisms.

The range in size in *Foaina exempta* is noteworthy. In the majority of preparations large specimens, surpassing in length most specimens of the associated *F. costata,* occur along with the very small ones, which are smaller than any *F. costata.* The morphological structure is the same throughout the range, however, and both the large and the small ones have the characteristic spherules and a short cresta. Even in the largest specimens the cresta length is usually only 4 or 5μ.

Living material was studied in *Neotermes insularis.* The body is clear, containing granules and spherules but no abundance of wood sufficient to give it a brown appearance, as in the other species of *Foaina* in the same host. The axostyle usually projects from the posterior end, often for a distance equal to half or somewhat more than half of the body length.

The movements of the flagellate are vigorous and very jerky. The movements are caused chiefly or entirely by the anterior flagella, which ordinarily are united almost to the end into a whip. The whip lashes as in *Devescovina,* the papilla meanwhile being moved laterally vigorously.

The trailing flagellum is a moderately stout cord usually three or four times the length of the body, turned in a long counterclockwise spiral. It is adherent to the body along its proximal portion in the region of the cresta. It is not undulated vigorously. In fact, in flagellates so slow-moving as to be followed closely it seems to be entirely passive, maintaining its spiral and bending with the movements brought about by the activity of the anterior flagella.

In small specimens the parabasal body is a bacilliform structure, like that of *F. solita,* along the dorsal side of the nucleus. In larger specimens the characteristic form is developed (fig. A, 5). There is a moderate length beyond the blepharoplast anteriorly, a sharp bend at the blepharoplast, and then the parabasal continues around the nuclear membrane and beyond it ventrally. In Delafield-stained material there sometimes seems to be a break at the angle near the blepharoplast, as if there were two separate parts; but actually the parabasal is a continuous structure. The slenderness of the parabasal filament is in marked contrast to the stoutness of the structure in *F. costata.*

The substance of the nucleus that fills all the space under the membrane is probably finely granular, though it appeared homogeneous in much material. It appears gray when the nucleus of *Devescovina* is black. At the periphery of the mass in the type material are a number of deep-staining granules (pl. 24, fig. 13), which vary in size. In most specimens the number ranged from 4 to 9, but some had fewer. Some of the granules are as large as the single nucleolus that is present in the typical *Foaina* nucleus. In other material of *F. exempta* the nucleus was of the structure typical in the genus.

The cytoplasm appears rather dense and homogeneous, compared to that of *F. costata.* No wood particles were observed, but most specimens contain numerous spherules that stain deeply with iron-haematoxylin. These spherules are not present in *F. costata.*

### **Foaina ovata** sp. nov.

Figure A, 6

*Type host.*—*Neotermes howa* var. *mauritiana* Sjöstedt. Mauritius.
T-4522. Mauritius. (Syntype slides TP-3202:6, 13, 4.)

*Additional hosts*
*Neotermes desneuxi* (Sjöstedt). Madagascar.
T-4452. Nampohana, near Fort Dauphin. (Homosyntype slide TP-3188:4.)
*Neotermes gracilidens* Sjöstedt. Madagascar.
T-4489. Perinet. (Homosyntype slide TP-3183:4.)
*Neotermes howa* (Wasmann). Madagascar.
T-4443. Manantantely, Madagascar. (Homosyntype slide TP-3167:26.)

*Diagnosis.*—(From type host): length 11.5 (6–19)$\mu$; width 7.5 (4.5–12)$\mu$; trailing flagellum a moderately slender cord; cresta slender, often difficult to distinguish from the proximal part of the trailing flagellum, length about 4–9$\mu$; parabasal body elongated, curved in a somewhat sigmoid form extending horizontally along one side of the nucleus and beyond it, fine filament passing to periphery of body but not turned posteriorly any great distance; trunk of axostyle projecting for a variable distance of a few microns, no cusplike enlargement at point of projection; flat capitulum moderately well developed; nucleus small, ellipsoidal, 1.5–3 × 1–2.5$\mu$; no adherent microörganisms.

*Foaina ovata* is the only devescovinid present in the four hosts listed above (p. 188). It was abundant on only a very small proportion of smears that were examined.

In the preparations of *Neotermes howa* var. *mauritiana* and *N. desneuxi* specimens of the larger sizes given in the diagnosis were present, but the length in the material from *N. howa* and *N. gracilidens* did not exceed 11$\mu$. Especially when the size is large, the form of the body is markedly ovoidal, but in general this species is not greatly different in form from other small species of *Foaina.*

The trailing flagellum is somewhat stouter than an anterior flagellum, but it is much more slender than that of *Foaina solita.* Since in almost all specimens the unusually slender cresta cannot be distinguished from the trailing flagellum, accurate measurement of its length is generally impossible. In larger specimens the full length of the cresta can sometimes be determined as 8–9$\mu$, and in small specimens it is probably only about half as much.

In shape the parabasal body, in larger specimens at least, is much like that of *Foaina nana,* but the free filament does not, as in that species, extend posteriorly at the periphery for a considerable distance.

The absence of an enlarged cusp is a characteristic feature of this species, and in no material examined have any rings been seen around the posterior part of the axostyle. The capitulum extends well beyond the limits of the nucleus on the sides and anteriorly.

Anterior to the capitulum and nucleus is a frequently more or less crescentic clear area. There are no conspicuous capitular granules.

A number of larger individuals on the type slides were in division stages. The paradesmose is slender, its diameter being comparable to that of the trailing flagellum. The specimens showed stages in the outgrowth of the new axostyles. A number of granules, of differing sizes, were present in the telephase nucleus, representing, perhaps, 5 or 6 chromosomes.

## **Foaina taeniola** sp. nov.

Figure A, 7

*Type host.—Paraneotermes simplicicornis* Banks.

T-316. Southern California. (Syntype slide TP-246:80.)

*Diagnosis.*—Length 23 (11–32)$\mu$; width 11 (7.5–17)$\mu$; trailing flagellum band-formed, maximum breadth about 1$\mu$, length about 65$\mu$; cresta length 14 (10–17)$\mu$; parabasal body elongated, with a J or sigmoid form, extending transversely or obliquely across the nucleus and beyond it to the periphery of the body; trunk of axostyle projecting 4–12$\mu$ in a pointed spike, little or no enlargement before projection, one or two deep-staining rings around the axostyle at the posterior end of the body; nucleus 4 (2.5–5) × 2.6 (1.6–4.1)$\mu$; no adherent microörganisms.

*Foaina taeniola* is seldom abundant in its host, and is not to be found at all on many slides. Even on the occasional slides where it is really numerous, its abundance is much less than that usual in devescovinids.

A characteristic in which this species differs from all other described species of *Foaina* is the markedly band-formed trailing flagellum. The trailing flagellum is also flattened in *F. acontophora,* but the band form is much more pronounced in *F. taeniola.*

The parabasal body has a short region anterior to the blepharoplast; this has the same diameter as the rest. There may be a rather sharp bend near the blepharoplast, but there is no second sharp bend at the posterior level of the nucleus, as there often is in *F. delicata* and *F. hamata.*

The small, close-fitting rings that are present surrounding the trunk of the axostyle near the point of projection from the body can be seen only in deep-stained material.

### **Foaina gracilis** Janicki

Figure A, 8, 9

*Foaina gracilis* Janicki, 1915, Zeitschr. wiss. Zool., 92:615, pl. 18, figs. 62–64.—Kirby, 1938, Quart. Jour. Micr. Sci., 81:3, pl. 1, figs. 1–4.

*Type host.—Neotermes connexus* Snyder. Hawaii.
T-305. (Bryant.) (Xenosyntype slides TP-199:7, 9, 6, 14.)

*Diagnosis.*—Length 24 (15–34)μ; width 13 (8–18)μ; rounded anteriorly, with an anterolateral indentation opposite the blepharoplast; not sharply pointed posteriorly; trailing flagellum a moderately stout cord; cresta slender, length 3–5μ; parabasal body closely applied to the nuclear membrane, extending on both sides of the blepharoplast, with the anterior section relatively long, encircling the nucleus almost completely in some specimens, partially in others; capitular granules not observed; trunk of axostyle stout, projecting from posterior end, enlargement at projection little or none; nucleus often 4.4–5.3 × 2.5–3μ; iron-haematoxylin-staining spherules usually present in cytoplasm; no adherent microorganisms.

This species, which has been found only in the one host, has already been described by me (1938*b*), in a revision of Janicki's account. The most important observation there reported was that of the single parabasal body, an observation disproving Janicki's claim that the parabasal apparatus consists of two separate bodies. As is brought out in the foregoing discussion of the genus *Foaina,* that observation has established the species as the type of a large genus, and has shown that *Janickiella* is a synonym of *Foaina.*

### **Foaina nana** (Kirby) comb. nov.

Plate 24, figures 14–23; plate 25, figures 24–25; figure A, 10

*Paradevescovina nana* Kirby, 1926, Univ. Calif. Publ. Zool., 29:114, fig. D, pl. 9, figs. 19, 20.
*Devescovina kirbyi* de Mello and de Brito, 1929, Arqu. Esc. Med. Cirurg. Nova Goa, ser. A, fasc. 5, p. 699, pl. 2, fig. C (*type host:* termite from Damaum, Portuguese India, incorrectly named *Coptotermes heimi*).

*Type host.—Cryptotermes hermsi* Kirby. Fanning Island.
T-9. (Syntype slide TP-2:1.)

*Additional hosts*

*Cryptotermes cynocephalus* Light. Java.
  T-4537. Buitenzorg. (Homosyntype slide TP-3224:7.)
*Cryptotermes darwini* Light. Galápagos Islands.
  T-335. (Light 1311 Ga.) James Island. (Homosyntype slide TP-275:4.)
*Cryptotermes domesticus* Haviland. Singapore.
  T-4589. (Homosyntype slide TP-3272:5.)
*Cryptotermes dudleyi* Banks. Panama.
  T-234. Ancon. (Homosyntype slide TP-151:1.)
  T-239. Balboa. (Homosyntype slide TP-159:3.)
  T-1013. Tanga, Tanganyika Territory. (Homosyntype slides TP-1024:24, 6.)
*Cryptotermes* sp. Java. (*C. dudleyi*, according to Emerson.)
  T-4556. Telawa. (Homosyntype slide TP-3234:11.)
*Cryptotermes* sp. Java. (Possibly *C. dudleyi*.)
  T-4572. Telawa. (Homosyntype slide TP-3235:3.)
*Cryptotermes fatulus* Light. Galápagos Islands.
  T-334. (Light 1306 Ga.) James Island. (Homosyntype slide TP-269:1.)
*Cryptotermes* sp. Tanganyika Territory.
  T-1035*a*. Amani. (Homosyntype slide TP-1037a:9.)
*Cryptotermes* sp. Tanganyika Territory.
  T-1041. Amani. (Homosyntype slide TP-1046:25.)
*Cryptotermes* sp. Kenya Colony.
  T-1086. Taveta Forest. (Homosyntype slide TP-1060:3.)
*Cryptotermes* sp. Kenya Colony.
  T-1091. Taveta Forest. (Homosyntype slide TP-1079:3.)
*Cryptotermes* sp. Madagascar. Mauritius.
  T-4506. Tamatave. (Homosyntype slide TP-3190:3.)
  T-4525. Reduit. (Homosyntype slide TP-3204:13.)
*Cryptotermes* sp. nov. Java.
  T-4553. Tapos. (Homosyntype slide TP-3237:5.)
*Kalotermes* (s. lat.) sp. Portuguese India (*"Coptotermes heimi."*)
  T-317. (De Mello.) Damaum. (Homosyntype slide TP-323:1.)
*Glyptotermes dilatatus* Bugnion and Popoff. Ceylon.
  T-318. (Cleveland. Collier.) (Homosyntype slide TP-263:7.)
*Glyptotermes taveuniensis* Hill. Fiji Islands.
  T-515. (Hill 4065.) (Homosyntype slide TP-515:6.)
*Glyptotermes* sp. nov. Java.
  T-4567. Bandjar. (Homosyntype slide TP-3229:7.)
*Glyptotermes* sp. Sumatra.
  T-4562. Kateman. (Homosyntype slide TP-3247:2.)
*Kalotermes condonensis* var. *chryseus* Hill. Australia.
  T-501. (Hill 3186.) A. C. T. (Homosyntype slide TP-501:32.)
*Kalotermes* (s. str.) sp. Madagascar.
  T-4341. Near Maevatanana. (Homosyntype slide TP-3110:7.)
*Kalotermes repandus* Hill. Fiji Islands.
  T-516. (Hill 4064.) (Homosyntype slide TP-516:3.)
*Neotermes connexus* Snyder. Hawaii.
  T-305. (Bryant.) (Homosyntype slide TP-199:2.)
*Neotermes dalbergiae* Kalshoven. Java.
  T-4532. Bandjar. (Homosyntype slides TP-3220:10, 17, 3.)
*Neotermes greeni* Desneux. Ceylon.
  T-310. (Cleveland. Collier.) (Homosyntype slide TP-253:109.)
*Neotermes larseni* Light. Cocos Island.
  T-322. (Light 1289 Co.) Wafer Bay. (Homosyntype slide TP-278:5.)

*Neotermes sonneratiae* Kemner. Java.
T-4574. Angke. (Homosyntype slide TP-3258:4.)
*Neotermes tectonae* Dammerman. Java.
T-4542. Telawa. (Homosyntype slides TP-3227:6; 3270:1.)
*Procryptotermes* sp. nov. Reunion.
T-4517. Pointe des Galets. (Homosyntype slide TP-3197:7.)
*Rugitermes kirbyi* Snyder. Costa Rica.
T-135. Cartago. (Homosyntype slide TP-76:20.)
T-148. Cartago. (Homosyntype slide TP-92:13.)
*Rugitermes panamae* Snyder. Panama.
T-120. Barro Colorado. (Homosyntype slides TP-59:3; 56:5.)
T-188. Barro Colorado. (Homosyntype slide TP-107:18.)

*Diagnosis.*—(From type host): length 12 (6–18)μ; width 6.5 (4.5–8.5)μ; trailing flagellum a moderately stout cord, 2–3 times the length of the body; cresta length 8.5 (6.5–10.5)μ; parabasal body with stout part along the dorsal side and posterior portion of the nucleus, and free parabasal filament extended to periphery and turned sharply posteriorly, often reaching to about the middle of the body; capitular granules abundant; axostyle somewhat enlarged before projection; nucleus 2–3 × 1.5–2μ; no adherent microörganisms. (From *Cryptotermes dudleyi*): length 17 (12–20)μ; width 7.5 (4–11)μ; cresta length 10 (8–11)μ; nucleus 2–3.5 × 1.5–3μ. (From *Rugitermes kirbyi*): length 18 (14–31)μ; width 6.5 (4–11)μ; cresta length 12 (9–13.5)μ. (From *Neotermes meruensis*): cresta length 6–10μ. (From *Kalotermes* T-4341): cresta length usually 6μ.

A small devescovinid from *Cryptotermes hermsi* was briefly described by me (1926) under the name *Paradevescovina nana.* Further study of this and other flagellates of the genus *Foaina* has made it clear that *Paradevescovina* is a synonym of *Foaina.* These studies have necessitated some modification of the original description, and have revealed the presence in many termites of flagellates that agree with *F. nana* in all structural characteristics.

De Mello and de Brito (1929) described three species of *Devescovina* from a termite collected at Damaum, Portuguese India. The third of these (species C, *Devescovina kirbyi*) was reported to be small and to possess a large tubular axostyle longer than the body. Most individuals had a length, including the projecting portion of the axostyle, of 12 to 20μ, and the length of the trailing flagellum usually was between 40 and 60μ. Examination of material sent to me by Colonel de Mello revealed two species of *Devescovina,* but the only organisms which could be the ones described as *Devescovina kirbyi* are species of *Foaina.* De Mello may have included *F. solita,* which is also present, in his account, but he doubtless made most of his observations on the more abundant and larger *F. nana.*

*Foaina nana* is a species of moderate size. The flagellates in the type host were below the average size of the species. Individual size differences are considerable, but not so considerable as de Mello and de Brito reported for "*Devescovina kirbyi.*" This, their species C, is said to have a length, without the projecting axostyle, of from 7 to 55μ, a width of 3 to 16μ, whereas, including the projecting axostyle, the length ranges from 12 to 88μ. Doubtless they included some measurements of the small *F. solita,* and the larger measurements certainly were not made on normal *Foaina.* The authors probably included some of the larger devescovinids, but even so they must have based some of these reports on abnormal specimens.

The papilla is large and when it is extended the body comes to a rounded point anteriorly. In this form it differs from such species as *F. gracilis,* with its broadly rounded anterior end. When the end of the papilla is lateral, the anterior end of the capitulum is oblique, and anterolateral to it is a well-marked clear area (pl. 24, figs. 17, 21–22). This area begins posteriorly near the posterior level of the nucleus, in the narrow space between it and the body wall. It broadens as it extends forward, then narrows as it approaches the tip of the papilla. There is much variation in the breadth of this clear area. Its outer boundary may be only the surface layer of the body. Its inner boundary is better defined, as the capitulum is bordered by small deeply staining granules. These are some of the capitular granules that are abundant in *F. nana.*

The trailing flagellum is a fairly stout cord of moderate length. There is some variation in its apparent stoutness. The few figures de Mello and de Brito gave of their species C show a broad trailing flagellum, which apparently is a band. Such a trailing flagellum occurs only on *Devescovina lemniscata* in the slide from their material examined by me, but the axostyle shown in the same figures could not be that of *D. lemniscata.* Those figures do not represent correctly any flagellate present in the material.

The cresta is slender and relatively more or less long. It is more variable in length than crestas of devescovinids usually are, and it is one character which creates some difficulty with the classification of flagellates from different hosts assigned to this species. Nevertheless, it has not been possible to subdivide this species on the basis of the cresta-length differences. The entire range found in the species is covered in the crestas of *F. nana* in certain hosts, or even on one slide, whereas in other hosts only part of the range is represented. In *Rugitermes panamae, R. kirbyi,* and many other hosts the cresta of *F. nana* varies a good deal in length and often reaches nearly or quite to the posterior end of the body. Variations in this length are shown in the figures of *F. nana* from *R. kirbyi* (pl. 24, figs. 15–18). In *Kalotermes* sp. T-4341, on the other hand, the cresta varies little in length and is uniformly short, not reaching posterior to the middle of the body. Its length is at the minimum of the range in the species. In *Cryptotermes* T-1091 the cresta is likewise uniformly short.

The chromatic element (pl. 25, fig. 24) was the only part of the parabasal apparatus seen by me when the original description was prepared. Typically it extends along the crestal surface of the nucleus to near the posterior end of this, bends and passes transversely across the posterior surface of the nucleus to the margin of the body, and then turns posteriorly, continuing for a variable distance. Often it reaches to the middle of the body in smaller individuals. It is a narrow band along the posterior surface of the nucleus, and anteriorly and posteriorly decreases in size to a filament.

Where this filament is in contact with the nuclear membrane, it borders on the achromatic substance of the parabasal body. Beyond the nuclear membrane the filament is free. There is usually no extensive section of the parabasal body anterior to the blepharoplast, on the anterior surface of the nucleus, as in *F. hamata.* In larger specimens, however, there may be some development of this anterior section.

The trunk of the axostyle is sometimes enlarged at the point of projection from the body. The enlarged cusp (pl. 24, fig. 22) is especially frequent in some material. In certain material, and some entire host infections, there is no enlargement, whereas in certain other hosts most material has a prominent cusp (for example, in *Cryptotermes dudleyi* T-1013).

Adherent microörganisms are absent from *F. nana* in all its hosts.

### **Foaina costata** sp. nov.

Plate 25, figures 26–29; figure A, 11

*Type host.*—*Neotermes insularis* Froggatt. Australia.
T-308. (Cleveland. Hill.) (Syntype slides TP-320:156, 210, 73.)

*Diagnosis.*—Length 23 (15–35)μ; width 11 (7–17)μ; trailing flagellum moderately stout; cresta length 17 (11–29)μ, often reaching to, or rounding, the posterior end of the body, at surface of body band-formed, reaching ⅔μ at maximum; parabasal body consisting of a C-formed part applied to the nuclear membrane and a stout filament, which extends free to the periphery and is turned posteriorly for a distance of several microns; capitular granules abundant; axostyle projecting a short distance from posterior end, with little or no enlargement before projection; nucleus 4 (3.2–4.6) × 2.7 (2.2–3)μ; no adherent microorganisms.

Living flagellates are very active, the whip of anterior flagella lashing, accompanied by movements of the papilla. Besides the jerky movements there is at times a vigorous vibration of one side of the body, apparently the side where the cresta is. There is a short, slender axostylar projection from the posterior end. The cytoplasm usually contains numerous rather large yellowish granular bodies and small fragments of wood, giving it a different appearance from that of *Foaina exempta* and *Devescovina lemniscata,* which are also present in *Neotermes insularis.*

The blepharoplast group consists of two or three granules. With these granules the two roots of the three anterior flagella connect, and the cresta is joined to one of them by a fine filament.

The anterior flagella are 1½ to 2 times the body length, and the trailing flagellum is about 2 or 3 times that length. The trailing flagellum is somewhat more slender than that of *F. nana,* follows the long cresta, and in living material seems to be attached to the surface for the length of the body. In fixed material it is clear that the attachment is slight, if there is truly any at all. Sometimes the flagellum runs parallel and close to the cresta, as if adherent to the surface of the body, though without the slightest indication of a membranous attachment. Often it is free in places, variously curved or looped away from the surface, and in many specimens it is entirely free except at its proximal attachment. The relationship of the trailing flagellum to the body surface is thus unlike the situation usual in *Trichomonas,* in which there is an attaching membrane keeping the position of the axoneme constant.

As seen from the side, at the edge of the body (pl. 25, fig. 27) the cresta is a narrow rod, which is somewhat expanded at the anterior end. When observed on the upper surface of the body (pl. 25, fig. 29), it appears as a more lightly stained band, often about ⅔μ broad at the middle, narrowing posteriorly to a filamentous terminal portion. The broadened anteromedial edge, seen when the cresta is at the edge of the body (fig. A, 11), is of about the same length as the breadth of the band.

In some specimens in fixed material the distal part of the stout parabasal filament extends into a projection from the body, or the end may project out of the cytoplasm. Normally, the filament turns posteriorly at the periphery (pl. 25, fig. 28), in many specimens for a distance of 5 or 6μ. The main substance of the parabasal body is thick, bluntly rounded without enlargement at its anterior end, and of uniform diameter for its whole length (fig. A, 11). The parabasal filament can be readily followed along the posterior side of the distal portion of the stout part, whence it continues free for a distance of several microns.

When the papilla is viewed flat, with the anterior flagella passing along its dorsal margin, the plate of capitular granules occupies almost its entire extent. The posterior part of the group of granules may extend over the anterior part of the nucleus, as viewed from above with the blepharoplast to the right of the observer (pl. 25, fig. 28). From this viewpoint the plate is convex toward the flagellate's left side. A prominent clear area is often visible between the anteroventral edge of the capitulum and the edge of the body (pl. 25, fig. 29; fig. A, 11).

The cytoplasm is ordinarily densely crowded with wood particles.

### **Foaina dogieli** (Duboscq and Grassé) comb. nov.

Plate 25, figures 30–31; figure B, 1–2

*Monocercomonas termitis,* partim, Comes, 1914, Boll. Accad. Gioenia Sci. Nat. Catania, (2) fasc. 33:15; non *Monocercomonas termitis* Grassi = *Hexamastix termitis.*

*Trichomonas dogieli* Duboscq and Grassé, 1923, C. r. Acad. Sci., 177:363.—Kirby, 1931, Univ. Calif. Publ. Zoöl., 36:197.

*Janickiella grassii* (stade *Trichomonas*) Duboscq and Grassé, 1924, C. r. Soc. Biol., 90:1444, figs. 9 and 10.

*Host.*—*Kalotermes flavicollis* (Fabricius). France.

T-323. (Emerson.) (Xenosyntype slides TP-197:7, 2.)

*Diagnosis.*—(After Duboscq and Grassé): length 12–16μ, large forms reaching 30μ; trailing flagellum adherent to body by all its proximal portion, following a thick internal rod (costa), from which it separates; parabasal body a long siderophile rod, generally transverse; numerous frontal granules forming a triangular field; axostyle prolonged posteriorly outside the body. (Original): length 18 (12–26)μ; width 9.3 (6–14)μ; trailing flagellum slender, length at least twice that of body; cresta narrow band-formed, length 16 (8–21)μ, often reaching to posterior end of body; parabasal body stout, elongated, following the posterior border of the nucleus transversely to the periphery of the body; capitular granules abundant; axostyle with little or no posterior enlargement, projecting several microns from the posterior end; nucleus 2.6 (2–3.5) × 1.7 (1–2.2)μ; no adherent microörganisms.

In their original description of *Foaina* (as *Trichomonas*) *dogieli,* Duboscq and Grassé recorded its length as 12–16μ, but later reported that it may reach 30μ. Its average length and width is about twice that of *Foaina grassii.*

The trailing flagellum (pl. 25, fig. 30) is much more slender than that of *F. grassii.* In its length of at least twice that of the body it is unlike the flagel-

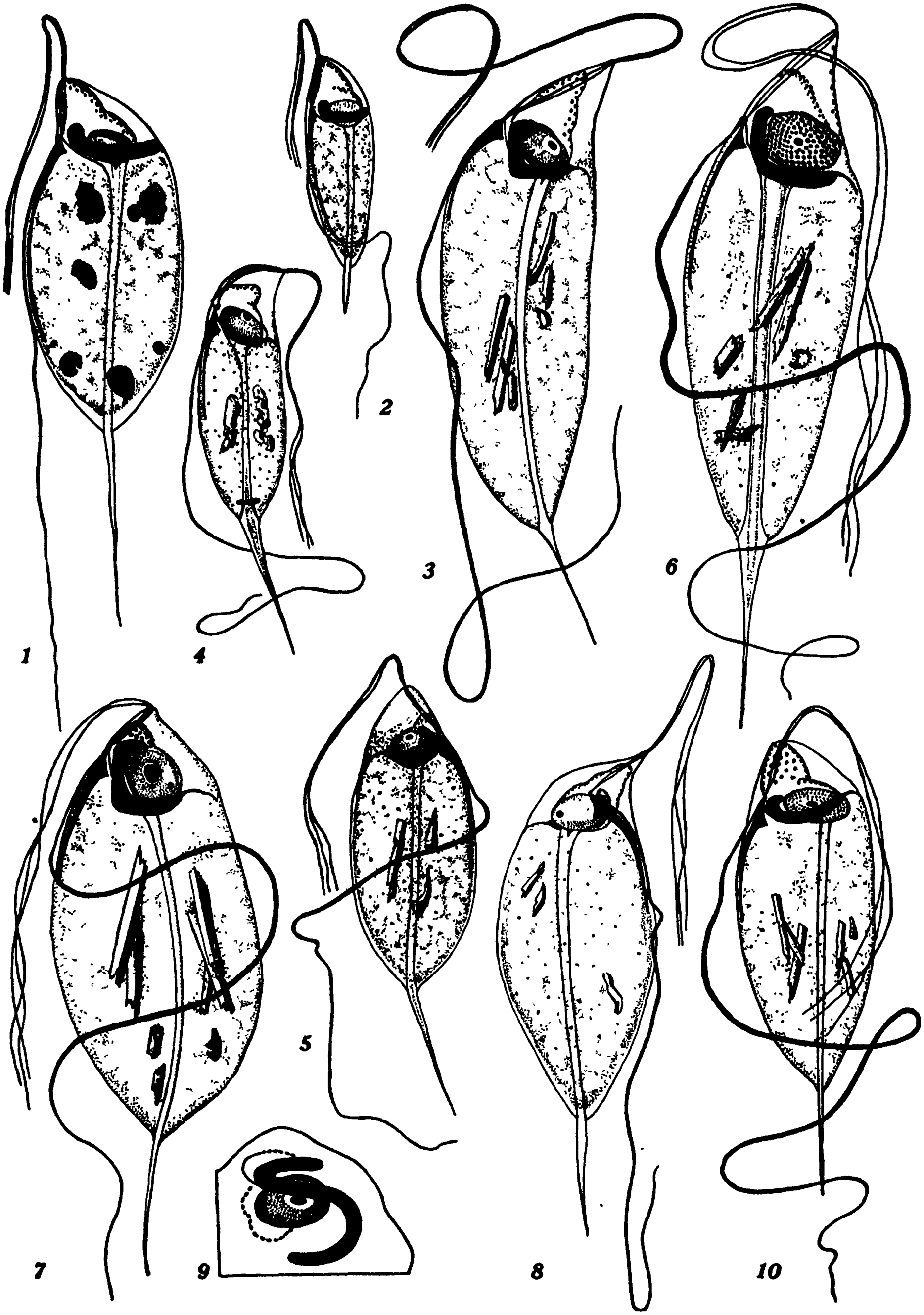

Fig. B. Species of *Foaina*. 1, 2. *F. dogieli* (Duboscq and Grassé) from *Kalotermes flavicollis*, Europe. 3. *F. hamata* sp. nov. from *Glyptotermes* sp. nov. T-2072, Uganda. 4. *F. minuscula* sp. nov. from *Procryptotermes* sp. nov. T-4359, Madagascar. 5. *F. delicata* Kirby from *Glyptotermes iridipennis*, Australia. 6. *F. acontophora* sp. nov. from *Cryptotermes* sp. T-3092, Zanzibar. 7. *F. signata* sp. nov. from *Kalotermes* sp. T-3025, Tanganyika. 8. *F. falcifera* sp. nov. from *Glyptotermes contracticornis*, Costa Rica. 9. *F. falcifera*, parabasal body in large specimen. 10. *F. funifera* sp. nov. from *Glyptotermes tuberculatus*, Australia. All figures, × 1750.

lum bordering the membrane of typical species of *Trichomonas*. In living material it apparently is adherent to the surface along the cresta, that is, for almost or quite the full length of the body. Duboscq and Grassé considered the proximal part of the trailing flagellum to be a true undulating membrane, and therefore put the flagellate in the genus *Trichomonas*. Its relation to the cresta differs in no way from that of the proximal portion of the trailing flagellum in other species of *Foaina*, in most of which the cresta, being shorter, bears less resemblance to the costa of *Trichomonas*.

In the relative sizes of cresta and trailing flagellum in species of *Foaina* there is no greater gap than that between the two species in *K. flavicollis: F. grassii* and *F. dogieli*. The former species has a stout trailing flagellum and a minute cresta; whereas the latter, with a very slender flagellum, has one of the longest crestas in the genus. These extremes are connected in the various species described in this paper, but no intergradation has been observed in the flagellates of *K. flavicollis*.

The apparent attachment is like that in all other Devescovininae; the process of fixation usually more or less breaks it, so that in prepared material the trailing flagellum often is free for part or all of its length. Duboscq and Grassé (1924) called attention to this detachment, which they regarded as the separation of the external border of the membrane from the internal border. In the species of *Trichomonas* in termites that have been studied by me, rupture of the undulating membrane in prepared material is comparatively infrequent. There is then no difficulty in recognizing a difference from the type of organization in *Foaina*. In *Tritrichomonas muris*, however, I have observed much more frequently a detachment of the flagellum bordering the membrane.

Unfortunately, division material of *Foaina dogieli* was not available for study. In other Devescovininae division stages show clearly that the cresta and trailing flagellum are entirely separate structures; and the mode of duplication distinguishes between cresta and costa.

My observations indicate that the expansion of the axostyle behind the nucleus shown in Duboscq and Grassé's figures is much exaggerated.

The parabasal body is stout and of even thickness for all its length. It curves around the nucleus against the membrane. In smaller specimens (pl. 25, fig. 31) it may not pass beyond the nucleus, but in larger ones (pl. 25, fig. 30) it usually extends toward the margin of the body opposite the cresta. The direction of its posterior portion is usually transverse or oblique.

## **Foaina hamata** sp. nov.

Plate 26, figures 32–33; figure B, 3

*Type host.—Glyptotermes* sp. nov. Uganda, Belgian Congo.
T-2072. Near Kampala. (Syntype slides TP-2023:24, 22; 2017:7.)
T-2090. Budongo Forest. (Xenosyntype slide TP-2028:9.)

*Additional hosts*
*Cryptotermes* sp. nov. Madagascar.
T-4403. Near Tulear. (Homosyntype slide TP-3151:1.)
T-4469. Near Ambovombe. (Homosyntype slide TP-3178:5.)

*Glyptotermes parvulus* Sjöstedt. Gold Coast.
T-301. (Silvestri.) (Homosyntype slide TP-318:1.)
*Glyptotermes caudomunitis* Kemner. Java.
T-4566. Bandjar. (Homosyntype slide TP-3242:18.)
*Glyptotermes* sp. (Probably *caudomunitis.*) Java.
T-4560. Bandjar. (Homosyntype slide TP-3212:2.)

*Diagnosis.*—(From type host): length 30 (15–40)μ; width 11.5 (6–17)μ; trailing flagellum a moderately stout cord; cresta length 8.5 (5–12)μ, anteromedial edge 1½μ in specimens of average size or above; parabasal body hook-formed, with longitudinal part and two transverse parts, the posterior often twice as long as the anterior and extended in a free filament to edge of body; axostyle with enlarged projecting cusp, projection often 6–13μ; nucleus 3.5–5.5 × 2–4μ; spirochaetes, many of which are 6–12μ long, usually adherent in a tuft to the posterior end of the body. (From *Glyptotermes parvulus*): length 36 (29–48)μ; width 18 (14–25)μ; cresta length 10.4 (8–12)μ, anteromedial edge often about 1μ; nucleus 5 (3.5–6) × 3 (2.5–3.5)μ; tuft of spirochaetes often adherent to the posterior end.

The compact blepharoplast group is composed of several granules.

The cresta is a well-developed structure of moderate length. It tapers gradually from an anteromedial edge that, for this genus, is fairly long. When observed at the surface of the body the cresta is not so markedly band-formed as that of *F. costata.*

The parabasal body (pl. 26, fig. 33) is curved close against the nucleus, with a sharp bend between the longitudinal part and each of the transverse parts. The shape is like that of the lower half of E, including the center bar, which is only about half the length of the posterior bar. The posterior bar passes along the margin of the nucleus on the left side just anterior to the posterior end. The angles at the outer edge are sharper than those at the inner edge, where the curvature is smoother to fit the nuclear membrane. The parabasal body, consequently, is thickest at those angles. The middle part of the longitudinal section is often the narrowest part of all. When stained in Delafield's haematoxylin, the parabasal substance usually contains small, clear, vacuole-like spaces of variable diameter, arranged in one or two irregular rows.

The parabasal filament is very clear in Schaudinn iron-haematoxylin material along the anterior margin of the posterior transverse section. It extends free beyond it for a distance of several microns to the periphery of the body (pl. 26, fig. 33). It does not turn sharply posteriorly as in some species, though it may be curved posteriorly to some extent. In material prepared by this method it could not be followed along the longitudinal limb, but in certain Flemming-Regaud preparations it was clearly visible for its whole extent. It does not follow the edge of the parabasal in the anterior part, but separates and passes directly to the blepharoplast, as has been observed in many other devescovinids.

The trunk of the axostyle is only moderately stout within the cytoplasm. At the posterior end it expands into a cusp (pl. 26, fig. 32) that sometimes is very large, though this enlargement was more restricted in the material observed from the type host than in that from some other hosts. Just before projection from the body some preparations from the type host showed a broad collar around the trunk.

Some specimens have no spirochaetes adherent to the body, but usually there are many on the posterior end. The extent of the area covered by spirochaetes varies. There may, at one extreme, be only a few spirochaetes adherent close to the cusp; at the other extreme a considerable part of the posterior half of the body is covered. The presence of this posterior group of spirochaetes characterizes *Foaina hamata* from all the hosts listed above, though there are more spirochaetes on flagellates from some than on those from other hosts.

### **Foaina minuscula** sp. nov.

Figure B, 4

*Type host.—Procryptotermes* sp. nov. Madagascar.
T-4359. Near Mahabo. (Syntype slides TP-3134:9, 3.)
T-4347. Near Mahabo. (Xenosyntype slides TP-3137:13, 5.)

*Diagnosis.*—Length 16 (12–19)$\mu$; width 5.5 (4–7)$\mu$; trailing flagellum a moderately stout cord; cresta length 5–7$\mu$; parabasal body curved against nuclear membrane, passing longitudinally and then transversely, with short free filament to periphery; trunk of axostyle with large cusp, often projecting 6–10$\mu$; nucleus 2.5–3.5 × 1.5–2$\mu$; few long spirochaetes adherent to posterior extremity.

*F. minuscula* was abundant in termites of all three colonies of *Procryptotermes* sp. nov. collected near Mahabo. It was absent, however, from two other colonies of the same species, one of which was found at Ankazoabo and the other near Maevatanana.

The flagellate is like the smallest individuals of *F. hamata.* There are, however, no specimens even approaching the average size of *F. hamata* on any of the many slides examined from three different colonies of termites. This very marked size difference seems to me to necessitate the recognition of *F. minuscula* as a separate species from *F. hamata,* in spite of the fact that it could not be distinguished morphologically from the smallest specimens of the latter species.

No parabasal bodies of the characteristic *hamata* form were observed. This fact is correlated with the smaller size, as small specimens of *F. hamata* also do not have the characteristic form of that structure.

The cusp of the axostyle is very prominent. A collar, like that in *F. hamata,* appears in heavily stained material at the base of the cusp. At the anterior end of this collar there is a well-defined, close-fitting ring.

The spirochaetes are like those on *F. hamata,* but they are not so abundant as is usual on that species. Their distribution is the same, however, as on some specimens of *F. hamata.*

### **Foaina delicata** Kirby

Figure B, 5

*Devescovina hilli* (young stages) Duboscq and Grassé, 1927, Arch. Zool. exp. gén., 66:459, text figures 3, 4; pl. 16, figs. 7–13.
*Foaina delicata* Kirby, 1928, Quart. Jour. Micr. Sci., 81:6, pl. 1, figs. 5–8.

*Type host.—Glyptotermes iridipennis* Froggatt. Australia.
T-304. (Hill.) (Syntype slides TP-309:3, 11, 18, 25.)
T-510. (Hill. Cléveland.) Barrington Top. (Homosyntype slide TP-510:86.)

*Additional hosts*

*Glyptotermes dubius* Hill. Australia.
T-511. (Hill 3232.) Ravenshoe, Queensland. (Homosyntype slide TP-511:66.)
*Glyptotermes perangustus* Hill. Australia.
T-512. (Hill. Cleveland.) Sydney.
*Glyptotermes neotuberculatus* Hill. Australia.
T-513. (Hill 3194.) Aust. Cap. Terr. (Homosyntype slide TP-513:1.)

*Diagnosis.*—Length 21 (15–28)μ; width 9.6 (5–13)μ; trailing flagellum a moderately stout cord; cresta length 10.7 (8–12)μ; parabasal body C-shaped or U-shaped, stout part closely applied to nuclear membrane, in part on its anterior surface dorsal to the blepharoplast; short, free parabasal filament at posterior end; capitular granules few; axostyle without marked posterior enlargement, with fairly long projection; nucleus 2–3 × 2–2.5μ; iron-haematoxylin-staining spherules often present; no adherent spirochaetes.

An account of this flagellate has already been published by me, together with comments on the original observations by Duboscq and Grassé (1927). A small proportion of specimens has been observed with microörganisms like *"Fusiformis hilli"* adherent to the surface. Most specimens, however, have no adherent microörganisms at all.

Some specimens have numerous spherules like those of *Foaina gracilis,* but there is usually also an abundance of particles of wood. Spherules of the same type have not been seen in *Foaina hilli.*

### **Foaina acontophora** sp. nov.

Plate 26, figure 35; figure B, 6

*Type host.*—*Cryptotermes* sp. Zanzibar.
T-3092. (Syntype slides TP-2064:1, 3.)

*Additional hosts*

*Cryptotermes* sp. Madagascar.
T-4303. Near Maevatanana. (Homosyntype slide TP-3095:9.)
T-4306. Ambongoamaranitra. (Homosyntype slide TP-3096:3.)
T-4375. Near Mahabo. (Homosyntype slide TP-3138:7.)
*Cryptotermes* sp. Madagascar.
T-4459. Manantantely, near Fort Dauphin. (Homosyntype slide TP-3168:7.)
*Neotermes castaneiceps* (Sjöstedt). Madagascar.
T-4505. Tamatave. (Homosyntype slides TP-3205:1, 14; 3191:12.)
*Neotermes* sp. nov. near *castaneiceps.* Madagascar.
T-4471. Near Ambovombe. (Homosyntype slide TP-3172:3.)
*Neotermes longus* (Holmgren). Madagascar.
T-4460. Manantantely. (Homosyntype slides TP-3181:22, 4.)
T-4484. Perinet. (Homosyntype slides TP-3184:4, 2.)

*Diagnosis.*—(From type host): length 31 (21–40)μ; width 14 (9–18)μ; trailing flagellum a narrow, thick band or stout cord; cresta slender, 12–17μ long; parabasal body and axostyle as in *Foaina hamata;* projection of axostyle often 10–20μ; nucleus 5.1 (4.1–7.5) × 4 (3.3–5)μ, often with a transverse curvature; adherent spirochaetes usually absent. (From *Cryptotermes* T-4375): length 36 (30–46)μ; width 17 (13–25)μ; cresta 12.5–18μ; nucleus 5.3 (4.1–6.7) × 4.2 (3.3–5.8)μ.

In size and many morphological characteristics *F. acontophora* resembles *F. hamata,* and it is often difficult to separate the two species positively.

In the type material the trailing flagellum is commonly flattened and about one-half micron wide at the maximum, whereas that of typical *F. hamata* is a moderately stout cord. But the band form of the trailing flagellum is less obvious in certain other material, and it is definitely a moderately stout cord in the Madagascar species of *Neotermes*.

The cresta is more slender anteriorly and is longer in *F. acontophora*. This difference is well marked in the type material of the two species, the cresta of *F. hamata* being 8–12μ long; that of *F. acontophora*, 12–17μ. In some material of *F. acontophora*, however, the cresta is shorter. The anteromedial edge of the cresta has a length of about 1½μ in average-sized specimens. The width decreases rapidly, becoming a filament in a distance of only about 2μ (pl. 26, fig. 35). The decrease is not so rapid in *F. hamata* (pl. 26, fig. 32).

The nucleus often has a curved form, like that observed in some material of *Foaina reflexa*, with a concavity on one side. This has not been observed in the nucleus of *Foaina hamata*, in which the longer axis is more definitely longitudinal.

Typical specimens of *F. hamata* have a tuft of spirochaetes at the posterior end of the body. There is no such tuft in *F. acontophora*.

The flagellates in the Madagascar species of *Neotermes* have been difficult to assign to species. The cresta is like that of the type of *F. acontophora*, and the trailing flagellum like that of the type of *F. hamata*. The nucleus, however, shows the transverse elongation and curvature observed in *F. acontophora*. There are no sufficiently definite differential characteristics for recognition of a new species, so assignment to *F. acontophora* seems to be the best solution of the problem.

### **Foaina signata** sp. nov.

Plate 26, figure 36; plate 27, figures 37–38; figure B, 7

*Type host.*—*Kalotermes* (s. str.) sp. nov. Tanganyika Territory.
T-3025. West of Ngorongoro Crater, at edge of Serengeti Plains. (Syntype slides TP-2044:10, 9, 3.)

*Additional hosts*

*Neotermes meruensis* Sjöstedt. East Africa.
T-2009. Near Arusha, T.T. (Homosyntype slides TP-1081:10, 12.)
T-3026. Near Ngorongoro Crater, T.T. (Homosyntype slides TP-2047:3; 2046:4.)
T-2045. Embu, Kenya. (Homosyntype slide TP-2008:9.)
T-2049. Meru, Kenya. (Homosyntype slide TP-2009:10.)

*Neotermes zuluensis* Holmgren. Transvaal.
T-4249. Near Warmbaths. (Homosyntype slide TP-3071:8.)

*Neotermes europae* (Wasmann). Madagascar.
T-4358. Near Malaimbandy. (Homosyntype slide TP-3122:12.)
T-4373. Near Mahabo. (Homosyntype slides TP-3140:15, 4, 1.)

*Diagnosis.*—(From type host): length 24 (12–33)μ; width 14 (9–20)μ; trailing flagellum a moderately stout cord; cresta length 7.6 (5–9)μ, anteromedial edge about 1–1.5μ; parabasal body hook-formed, with anterior portion along anterior surface of nucleus, two sharp bends, posterior part at or near posterior level of nucleus, extended in free filament that curves posteriorly; trunk of axostyle relatively slender, enlarged very little at the point of projection from the body, no greatly expanded cusp, pointed projecting spike 4–9μ; nucleus ellipsoidal or spheroidal, 2.5–5.8 × 2.5–5μ, often with narrow, clear space under membrane, homogeneous nuclear mass with one to several peripheral nucleoli and a relatively large, deep-staining body composed of 5 or 6 granules; no adherent spirochaetes;

**ring-formed structures about ½μ in diameter, staining with Delafield, unevenly distributed on surface of all individuals. (From *Neotermes meruensis*): surface rings fewer and larger, many about 1μ in diameter, with a spherical substance extending below each ring into the cytoplasm. (From *Neotermes europae*): length 38 (25–47)μ; width 17 (12–28)μ; cresta length 7.6 (5.8–10)μ; projecting axostyle 4–12μ; nucleus 2.5–5.8 × 2–4μ; width 17 (12–28)μ; surface rings small.**

The parabasal body (fig. B, 7) resembles that of *F. hamata*. It borders the nucleus on three sides, bending sharply at two points, not being gradually curved in a C form as in some species of the genus. It is rather like the lower part of an E, including the center bar, which latter is about half the length of the lower bar. The shorter bar extends across the anterior surface of the nucleus, and the blepharoplast is close to the anterior angle. The longitudinal part is also closely applied to the nuclear membrane; then it turns sharply transversely. The posterior transverse bar is usually entirely near the level of the posterior end of the nucleus, but occasionally it is curved forward as far as the middle level, on the right side of the nucleus.

The parabasal filament extends beyond the end of this transverse bar to the periphery of the body, where often it ends. Sometimes it turns posteriorly for a short distance. The filament becomes separate from the longitudinal part of the parabasal, and runs directly to the blepharoplast, passing close to the cresta (fig. B, 7).

The capitulum of the axostyle was demonstrated best in material from the Madagascar *Neotermes* fixed in Hollande's fluid. In large individuals so prepared it was seen to be well developed, being as broad as the body and curved so that there is an opening measuring less than a quarter of the circumference. It is in marked contrast to the flat capitulum of *Devescovina glabra* of the same host.

In larger individuals the trunk of the axostyle has a thickness of about one micron for most of its length through the body. The diameter a few microns anterior to the posterior end of the cytoplasm is somewhat more than half that immediately posterior to the nucleus. Just before emerging from the body it expands a little, but not enough to exceed the diameter of the more anterior part of the trunk. A black band is demonstrated in appropriately prepared material around this slightly enlarged part. Outside the cytoplasm there is a free projecting spike which tapers to a filament. No greatly expanded cusp like that of *Foaina hamata* has been seen in any one of hundreds of specimens observed.

The nucleus (pl. 26, fig. 36) has some unusual characteristics by which alone it is possible to distinguish *F. signata* from other species of *Foaina*. The same nuclear characteristics have been seen in the species from all the host termites. The nucleus is ellipsoidal in shape, being sometimes almost spherical, sometimes almost twice as long as wide. In most Schaudinn-fixed material there is a clear space between the membrane and the central mass. In Flemming-fixed material the space, though less evident, is nevertheless often present. The other species of *Foaina* in the same hosts shows no such space, whatever the fixative used. The ground substance of the central mass usually appears homogeneous (pl. 26, fig., 36, *a, c*), but sometimes is resolved into a finely granular structure (fig. 36, *e*). In *F. signata* there are two sorts of intranuclear material besides this ground substance. At some point on the periphery of the mass, and set apart from it by a narrow clear space, is a deep-staining spheroidal body, of small but variable size. Sometimes there are two or three such granules, each smaller in size than a solitary one. These correspond to the nucleoli described in other species. Embedded in the ground substance and always so situated that one of its edges is at the periphery of the mass, is a spheroidal body whose diameter often amounts to about a third that of the mass. It stains less intensely than the nucleolus, but may appear as a homogeneous spherule in heavily stained material. On suitable differentiation it may be observed that there are five or six separate granules arranged in a group set off by a clear space from the surrounding nuclear substance. If the granules are embedded in a matrix, this is not so deep-staining as is the so-called homogeneous substance of the nucleus.

A unique characteristic of *F. signata* is the presence of small, unevenly distributed rings on the surface. In the type host, though subject to a limited variability in size, many have a diameter of about half a micron (pl. 27, fig. 37). They are especially conspicuous in certain Schaudinn-Delafield material, in which they stain as deeply as does the parabasal body. They may also be well stained in certain iron-haematoxylin material, but are not so conspicuous. In surface view they appear as minute, relatively thick rings with a small clear space in the center. In side view they are flat bars, with the flat side applied to the surface of the body. It is unlikely that these bodies are actually open rings, but rather that the central material does not stain by the methods used. They are moderately numerous on all individual flagellates, but are unevenly distributed. They may be present on any part of the body. They are not present on any other flagellates in the hosts of *F. signata.*

The material from the other hosts was less favorable, because of less fortunate staining conditions, for study of the rings. In *F. signata* from *Neotermes meruensis,* rings were recognized on many specimens, and probably are present on all. They were larger, however, in many instances having a diameter of a micron (pl. 27, fig. 38). All those observed on flagellates from the type host were small, and all those on flagellates from *N. meruensis* T-2009 were large. On flagellates from *Neotermes meruensis* T-3026, however, both small and large ones were found. Many smaller ones seemed solid, not showing the ring structure. On the Madagascar specimens there were small rings only, but the preparations were not good for study of these, and they would probably have been overlooked without the clue afforded by observations on flagellates from other hosts.

In the flagellates from *Neotermes meruensis* T-3026 (pl. 27, fig. 38) these structures appear to have a more intimate relationship to the flagellate than that of mere surface adherence. In optical section, a slightly curved, deep-staining bar is present at the periphery of the body, projecting from it as if it were a flat disk on the surface. Adjacent to the bar within the cytoplasm, however, there is a spheroidal structure which stains less deeply but is nevertheless well defined. Thus the ring appears to be merely the external part of a structure which is mostly enclosed in the body. There are only a few of the structures on each of the flagellates, and they are unevenly distributed.

In flagellates from the type host the rings, which are smaller, seemed to be simply adherent loosely to the surface, with no spheroidal part extending into the cytoplasm (pl. 27, fig. 37). They were readily detached in damaged specimens. The occasional occurrence of two rings closely applied to one another, and perhaps united, suggests the possibility of fission.

It is more likely that these rings are epibiotic microörganisms than that they are structures of the flagellates. Whether or not there are two kinds on *Foaina signata* from different hosts remains a question.

Structures about 2–3 × 5–6μ, with thick brown walls, were numerous in the gut contents of all preparations from the type host. These were often present in the cytoplasm of *F. signata,* along with particles of wood.

## **Foaina falcifera** sp. nov.

Plate 27, figures 39–43; figure B, 8, 9

*Type host.*—*Glyptotermes contracticornis* (Snyder). Costa Rica. T-132. Cartago. (Syntype slides TP-72:17, 18, 5.)

*Additional host.*—*Glyptotermes montanus* Kemner. Java. T-324. (Cleveland. Collier.) (Homosyntype slide TP-262:11.)

*Diagnosis.*—(From type host): length 21 (13–37)μ; width 10.5 (5–19)μ; trailing flagellum a moderately stout cord about twice the length of the body; cresta length 8.3 (6–11)μ, anteromedial edge 1½μ; parabasal body in larger specimens with rather long transverse portion, nearly reaching the periphery of the body, free parabasal filament comparatively short; axostyle with little or no posterior enlargement, often surrounded before projection by a siderophile collar, projection often up to 5μ, occasionally 8–12μ; nucleus ellipsoidal, 5.4 (4.6–6.1) × 2.8 (2.2–3.2)μ in larger specimens; spirochaetes about 8–10μ long sometimes adherent to posterior end. (From *Glyptotermes montanus*): length 22 (18–27)μ; width 12.5 (8.5–17)μ; scattered spirochaetes usually adherent over all the surface.

The parabasal body is often somewhat sigmoid in form. It bends around the dorsal part of the nucleus, and the blepharoplast is close to a point on the bend. Turning at the posterior level of the nucleus, it often extends obliquely anteriad toward the ventral side, but may continue transversely at or near the posterior level, as is characteristic of *F. hamata.* A characteristic of this parabasal is the fact that in larger individuals the stout part does not terminate near the nuclear membrane, but often continues to the periphery of the body (pl. 27, figs. 39, 41, 43). This distal part is often curved posteriorly, in opposition to the proximal part, giving the sigmoid shape (fig. B, 9). At the end of the parabasal is a comparatively short, free filament (fig. B, 8) which usually turns posteriorly at the edge of the body.

In Delafield-stained material there is sometimes visible a row of deeply stained granules in the parabasal (fig. 27, fig. 40), like those in *Trichomonas termopsidis.* More frequently there are small, clear vesicles in a stainable matrix, usually arranged in two uneven rows.

The nucleus is somewhat elongated, but is not curved like that of *F. acon-*

*tophora, F. reflexa, F. funifera,* and other species. The chromatin mass may be extended in a point along the trunk of the axostyle.

*Foaina falcifera* is closely related to *F. hamata.* Although the cusp of the axostyle is typically prominently enlarged in *F. hamata,* and only a little enlarged in *F. falcifera,* there are some specimens of the former that are like the latter species in this respect. The chief difference is in the parabasal body, which in *F. hamata* seldom extends far beyond the limits of the nucleus in a sigmoid form, as is characteristic of fully developed *F. falcifera.* In smaller specimens of *F. falcifera,* however, the parabasal is like that of *F. hamata.*

### **Foaina funifera** sp. nov.

Figure B, 10

*Type host.—Glyptotermes tuberculatus* Froggatt. Australia.
T-4608. (Hill. Cleveland.) (Syntype slides TP-3284:21, 23, 38.)
T-507. (Hill 3187.) (Xenosyntype slide TP-507:6.)

*Additional host.—Cryptotermes queenslandis* Hill. Australia.
T-519. (Hill 3492.) (Homosyntype slide TP-519:17.)

*Diagnosis.*—Length 21 (14–28)μ; width 11 (8–15)μ; trailing flagellum a very stout cord, length usually 55–60μ; cresta length 9 (7–10.5)μ, anteromedial edge about 1–1½μ; parabasal body sigmoid in form, passing posteriorly, transversely, then usually obliquely anteriorly again to near the anterior level of the nucleus, ending in a free filament that curves posteriorly at the periphery; trunk of axostyle comparatively slender, projecting, with little or no previous enlargement, often 3–8μ; nucleus much elongated, narrow, often markedly curved in a more or less transverse direction, 3.5–5.5 × 1.5–2.5μ, finely granular chromatin with a very small nucleolus; cytoplasm containing a variable number of moderate-sized spherules that are brown in Schaudinn-Heidenhain preparations; no adherent microorganisms.

The trailing flagellum of *Foaina funifera* is an unusually stout cord; it is much stouter than that of *F. falcifera,* which the species resembles in some respects.

The parabasal body (fig. B, 10) is curved around the dorsal side of the nucleus, near the blepharoplast; passes transversely for some distance at the posterior level of the nucleus; then extends obliquely anteriorly, reaching again the anterior level of the nucleus. The more voluminous substance does not extend much, if any, beyond the edge of the nucleus; but the parabasal filament extends beyond it to the periphery of the body and turns posteriorly. The parabasal filament first appears distinctly along the edge of the distal half of the parabasal body. The greater part of the free filament is at the very edge of the body; in some specimens on smears the contour of the body is altered in this region, owing to its presence. Instead of curving posteriorly, the terminal part of the filament may extend straight out in a cytoplasmic protuberance; in some specimens, in fact, the filament seems to project freely out of the cytoplasm. Occasionally, although the normal position of the filament in the cytoplasm has not been altered, there is a rounded cytoplasmic protuberance. Evidently, the parabasal filament is a firm, elastic structure which resists the changes in form of the flagellate that may be induced by the technical treatment.

The shape of the nucleus is unusual. It is elongated (fig. B, 10) and markedly curved, the length (taken around the curve, instead of across it as in the diagnosis) being at least three times the width. The deep-staining peripheral nucleolus is unusually small.

The cytoplasm contains numerous small fragments of wood, small deep-staining granules, and a variable number of moderate-sized spherules. The spherules, which are brown in Schaudinn-Heidenhain material, resemble, except in size, the larger spherules of many oxymonads.

Together with *Foaina funifera* there are smaller flagellates of the same genus, mostly under 10$\mu$, with an ellipsoidal nucleus and a shorter cresta. In them the cytoplasm has a different texture, being free from the brown spherules and numerous fragments of wood. Often there are numerous, deep-staining, rounded or irregular bodies. They have been identified with *F. solita.*

### **Foaina reflexa** sp. nov.

Plate 28, figures 44–49; figure C, 1

*Type host.*—*Kalotermes perezi* Holmgren. Cartago, Costa Rica.
T-141. (Syntype slides TP-88:14, 15.)
T-149. (Xenosyntype slide TP-95:5.)
T-144. (Xenosyntype slide TP-86:17.)
T-133. (Xenosyntype slide TP-73:2.)

*Additional hosts*
*Calcaritermes brevicollis* Banks. Panama.
T-206. Barro Colorado. (Homosyntype slides TP-118:10; 121:2.)
T-125. Same locality. (Homosyntype slide TP-60:5.)
*Calcaritermes emarginicollis* Banks. Costa Rica.
T-171. Estrella. (Homosyntype slide TP-106:25.)
T-158. Same locality. (Homosyntype slides TP-100:3, 9.)
*Calcaritermes nearcticus* Snyder. Florida.
T-531. Bartow. (E. M. Miller.) (Homosyntype slide TP-534:2.)
*Calcaritermes parvinotus* Light. Mexico.
T-265. (Light 183 Me.) (Homosyntype slide TP-225:7.)
*Cryptotermes breviarticulatus* Snyder. Panama.
T-230. Taboga Island. (Homosyntype slides TP-141:11, 2.)
*Cryptotermes cavifrons* Banks. Florida.
T-533. Key Large. (Emerson.) (Homosyntype slide TP-536:2.)
*Cryptotermes longicollis* (Banks.) Panama.
T-223. Taboga Island. (Homosyntype slides TP-137:38, 8.)
*Cryptotermes havilandi* (Sjöstedt). Swaziland; Portuguese East Africa.
T-4003. Beira. (Homosyntype slide TP-2066:15.)
T-4260. Near Bremersdorp. (Homosyntype slide TP-3077:5.)
T-4006. Lourenço Marques (Homosyntype slide TP-2069:1.)
*Kalotermes jeannelanus* Sjöstedt. East Africa.
T-1064. Moshi, T. T. (Homosyntype slide TP-1056:3.)
T-2088. Near Hoima, Uganda. (Homosyntype slide TP-2027:6.)
*Kalotermes* (s. str.) sp. nov. Tanganyika Territory.
T-3025. Near Ngorongoro Crater. (Homosyntype slides TP-2044:11, 7.)
*Kalotermes* (s. str.) sp. nov. Portuguese East Africa; Swaziland.
T-4000. Beira. (Homosyntype slide TP-2065:23.)
T-4277. Near Bremersdorp. (Homosyntype slide TP-3084:1.)
*Neotermes castaneus* Burmeister. Florida.
T-530. Pine Crest. (Homosyntype slide TP-533:25.)

*Neotermes erythraeus* Silvestri. Eritrea.
T-312. (Silvestri.) (Homosyntype slide TP-321:1.)
*Neotermes holmgreni* Banks. Panama.
T-222. Taboga Island. (Homosyntype slides TP-134:14; 130:6.)
*Neotermes meruensis* Sjöstedt. East Africa.
T-2009. Near Arusha, T.T. (Homosyntype slide TP-1081:3.)
T-2045. Embu, Kenya. (Homosyntype slide TP-2010:24.)
T-3026. Near Ngorongoro Crater. (Homosyntype slide TP-2046:12.)
*Neotermes zuluensis* Holmgren. Swaziland; Transvaal.
T-4276. Nsoka. (Homosyntype slides TP-3083:4, 6; 3091:2.)
T-4249. Near Warmbaths. (Homosyntype slide TP-3071:7.)
*Neotermes europae* (Wasmann). Madagascar.
T-4358. Near Malaimbandy. (Homosyntype slide TP-3146:7.)
*Neotermes* sp. Tanganyika Territory.
T-2012. Mount Meru. (Homosyntype slide TP-1085:17.)
*Kalotermes* (s. lat.) sp. nov. Kenya Colony.
T-2000. Lake Chala. (Homosyntype slide TP-1078:19.)
*Kalotermes* (s. lat.) sp. nov. Transvaal.
T-4240. Nylstroom. (Homosyntype slides TP-3069:18, 6.)
T-4252. Duivel's Kloof. (Homosyntype slide TP-3072:11.)

*Diagnosis.*—(From type host): length 24 (17–40)μ; width 12 (9–18)μ; trailing flagellum a moderately stout cord; cresta narrow, length 14 (11–17)μ, anteromedial edge at most 1μ or a little more; form of parabasal body distinctive, longitudinal section along dorsal side of nucleus usually to posterior end of this, then turned anteriorly again, forming a U, and passing transversely usually near the anterior level of the nucleus, or obliquely posteriorly, free filament extended to margin of body; capitular granules abundant; posterior end of axostyle usually with moderately enlarged cusp, projecting often 5–10μ; nucleus 3.2 (3–4) × 2.4 (2–3)μ; spirochaetes commonly present attached near the anterior end, some also often attached at the posterior end. (From *Calcaritermes brevicollis*): length 19 (12–31)μ; width 8.5 (6–17)μ; cresta 6–17μ; nucleus 2.4 (1.5–3.5) × 2 (1–3.5)μ. (From *Cryptotermes breviarticulatus*): cresta length usually 6–9μ. (From *Kalotermes* T-4000): length 13–25μ; width 6–19μ; cresta 6–13μ. (From *Kalotermes* T-3025): length of trailing flagellum 60–70μ; projection of axostyle often 8–12μ.

*Foaina reflexa* is a species of moderate or large size. Usually there are in a host no very small individuals of the same species. In *Cryptotermes* T-4260, for example, the majority of flagellates had a length of about 35μ, and the smallest specimen seen was 19μ long. In preparations from *Kalotermes* T-3025 the majority of specimens measured 20–25μ, and the smallest had a length of 13μ. In *Calcaritermes brevicollis,* however, small individuals were particularly numerous, in relation to the large form, bringing the average measurements lower.

The form of the parabasal body is a distinctive characteristic of this species, though it varies to some extent. The proximal part extends longitudinally along the dorsal side of the nucleus (pl. 28, fig. 45). After reaching the posterior level of the nucleus, the parabasal turns forward and extends to near its anterior level, then passes more or less transversely to the margin of the body. The part of the parabasal near the blepharoplast thus has a U-formed bend (pl. 28, fig. 46). There is variation in the sharpness of the bend; sometimes the U is somewhat straightened out (pl. 28, fig. 47); but there is always a bend anteriorly so that the middle part of the parabasal is typically anterior to, or at the anterior level of, the nucleus.

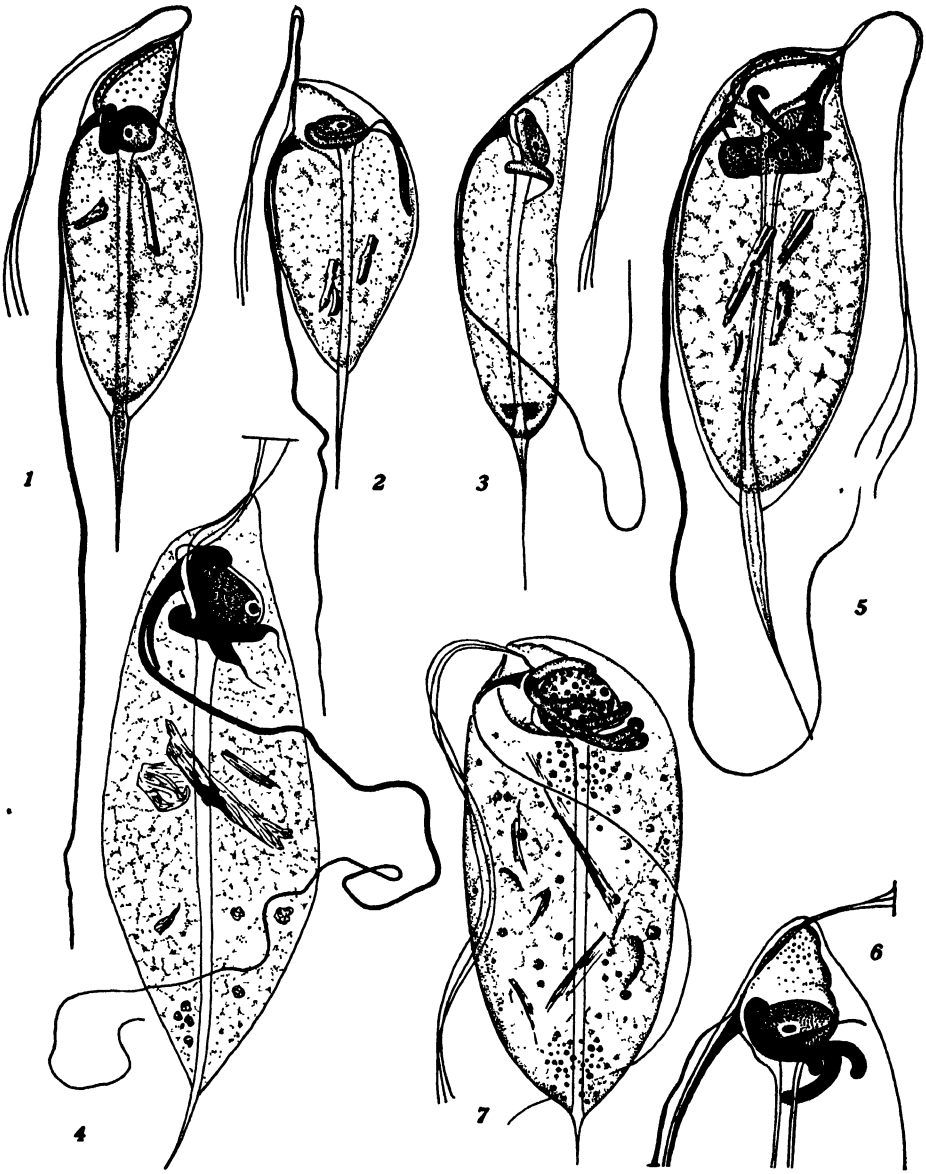

Fig. C. Species of *Foaina*. 1. *F. reflexa* sp. nov. from *Kalotermes perezi,* Costa Rica. 2. *F. appendicula* sp. nov. from *Glyptotermes minutus,* Ceylon. 3. *F. duo* sp. nov. from *Glyptotermes niger,* Java. 4. *F. hilli* (Duboscq and Grassé) from *Glyptotermes iridipennis,* Australia. 5. *F. nucleoflexa* sp. nov. from *Cryptotermes merwei,* South Africa. 6. *F. ramulosa* sp. nov. from *Cryptotermes* sp. nov. T-4403, *Madagascar.* 7. *F. pectinata* sp. nov. from *Anacanthotermes ochraceus,* Egypt. All figures, × 1750.

The parabasal filament is a heavily staining structure that appears clearly at the edge of the parabasal beginning at the bottom of the U. The proximal part, which joins the blepharoplast, is more inconspicuous. The conspicuous part of the filament, which sometimes is the only part of the parabasal body that is visible, often has more or less the form of a hook, extended transversely across the body with the back anterior. The bent hook part extends around the dorsal margin of the nucleus. The shaft continues in some degree the same curvature, with the concave side posterior. At the margin of the body there is no sharp bend posteriorly. Sometimes the whole shaft, beginning near the U, is bent more posteriorly, so that its direction is even longitudinal and the end of the filament is far posterior to the nucleus (pl. 28, fig. 48); but generally it is more or less transverse. The parabasal body never has the form of that of *F. nana* or *F. hamata.*

An unusual appearance was presented by certain preparations of *Foaina reflexa,* from *Neotermes castaneus,* that had been fixed in Hollande's fluid and stained in protargol (pl. 28, fig. 49). The part of the parabasal adjacent to the nucleus, which stains with iron-haematoxylin after Champy's fluid, could not be distinguished. The parabasal filament, described in the preceding paragraph, was very well defined and was formed as a band that attained a breadth of 1.5–2$\mu$ in large specimens. At its proximal end this band was obtusely pointed and sharply bent; it retained the band form nearly to the distal end, where it was bluntly pointed. The band, furthermore, did not appear simple and flat; but a frilled narrow membrane appeared to extend from its inner side near one edge. The silver-impregnation technique was used in study of only this species of *Foaina,* so it is not known how this structure compares with that of other species.

The clear area (pl. 28, figs. 47, 48) anterolateral to the capitulum is often prominent in this species, though it is not to be observed in all specimens.

In the type material the posterior end of the trunk of the axostyle was enlarged in a moderate-sized cusp in all specimens (pl. 28, fig. 45). This enlargement, however, is not always to be found in the species. No specimens observed in *Calcaritermes brevicollis,* small or large, had so prominent a cusp as that in the type specimens. Often, especially in small flagellates, there was no enlargement at all. In *Kalotermes* T-3025, likewise, the specimens observed had no prominently developed cusp, though often there was some enlargement. In certain other hosts (*Kalotermes jeannelanus, Kalotermes* T-4000, *Cryptotermes* T-4260) the cusp was prominently developed in most specimens, whereas in some (*Neotermes meruensis, Kalotermes* T-2000) the cusp was well developed in some individual flagellates and not in others on the same slide. The development of the terminal part of the trunk of the axostyle is a variable characteristic in the species.

In many specimens, both from the type host and others, the nucleus has been observed to be curved in a transverse radius, like that of *F. nucleoflexa.* The nucleus is much smaller, however, and the curvature is less conspicuous than in that species. On the broadest side the nucleus has an ellipsoidal or somewhat rectangular outline. In the majority of preparations the nuclei were so heavily stained that the curvature could not be seen at all, and this form of nucleus is not a universal characteristic of *F. reflexa.*

Spirochaetes are often adherent to the anterior and posterior ends. There usually are at least some present, especially at the anterior end, though some specimens lack them. They are more abundant in the material from some hosts (e.g., *Kalotermes jeannelanus*) than from others (e.g., *Calcaritermes brevicollis,* in which there were found few adherent spirochaetes, or none at all). Near the anterior end the group of spirochaetes adheres to a restricted area of the body surface near the first part of the parabasal body beyond the U bend.

*F. reflexa* usually contains an abundance of wood fragments.

## **Foaina decipiens** (Grassé)

Fig. D

*Parajoenia decipiens* Grassé, 1938, Bull. Soc. Zool. France, 63:113, fig. 1-A, B, C.

*Type host.—Neotermes aburiensis* Sjöstedt. Ivory Coast.

*Diagnosis.*—(After Grassé): length 23–40μ; three slender anterior flagella; stout trailing flagellum; short cresta (length not given, shorter than nucleus, 3.5μ, according to magnification of figure); parabasal body applied to the nucleus; frontal granules numerous in the rostrum; cytoplasm containing many wood particles and chromatic granules; tuft of 15–50 spirochaetes 10–40μ long constantly adherent to an area of the body surface near the nucleus; spirochaetes often adherent to the posterior end.

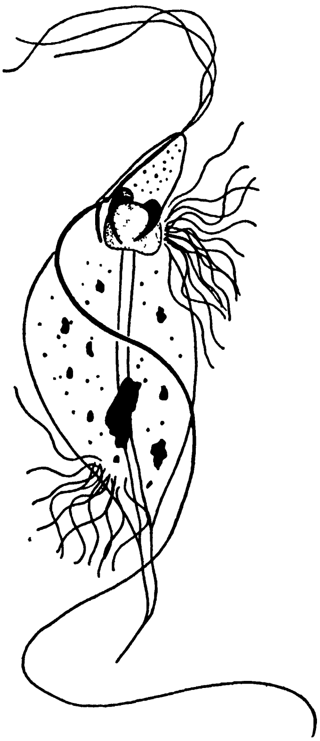

Fig. D. *Foaina decipiens* (Grassé) from *Neotermes aburiensis,* Ivory Coast. The two comma-shaped structures applied to the nuclear membrane probably are parts of one continuous U-shaped parabasal substance, belonging to a parabasal apparatus that possibly is like that of *Foaina reflexa.* × approx. 1750. (After Grassé, 1938.)

I have not seen this species of *Foaina,* and therefore cannot exactly compare it with the other species. Comparison of Grassé's description with the characteristics of the twenty-two species I have studied showed it to be identical with none, but suggested a relationship between his flagellate and *F. reflexa. F. reflexa* is present in the East African hosts from which I have described *Caduceia theobromae, Caduceia nova,* and *Pseudodevescovina ramosa;* Grassé's species is associated with *Caduceia theobromae* and very similar forms of *Pseudodevescovina.* The peculiar distribution of the adherent spirochaetes, noted by Grassé, agrees exactly with the pattern in *F. reflexa.* There is similarity between the two flagellates in size and in the trailing flagellum and the axostyle. The cytoplasm of *F. reflexa* also contains a large amount of wood, in agreement with what Grassé noted in his diagnosis of *Foaina decipiens.*

In comparing the two forms, however, there is more difficulty with the parabasal body and cresta. Grassé supposed that two dissimilar parabasal bodies are attached to the nuclear membrane, and that only one of the two is united to the blepharoplast. His figures (fig. D) show them as bodies that are entirely separate; but they are in a position that makes it clear to me that they are actually parts of the same parabasal. Such a double structure as he described does not exist in any devescovinid or other flagellate that I have seen. Grassé was evidently misled in his interpretation by the partial separation of parts of the parabasal that is not infrequent in preparations. The parabasal shown in his figure 1-A, however, assuming the two parts to be united, bends forward in the manner characteristic of *F. reflexa.*

The cresta as described in *F. decipiens* is much shorter than I have ever observed that in *F. reflexa* to be. Such a short cresta has been seen by me only in the species *Foaina grassii, F. solita, F. parvula, F. exempta,* and *F. gracilis.* The first three of these seldom attain even the minimum size of *F. decipiens;* and the last two differ at least in the scarcity of wood, the presence of spherules, and the absence of adherent microörganisms. These two are each restricted, furthermore, to only one host each, whereas *F. reflexa* is a very widespread species. In my experience, the cresta is often not so clearly demonstrated after osmic fixation as after Schaudinn's. The possibility that Grassé's observations on the cresta were not complete is further suggested by the fact that, presumably in the same series of preparations, he overlooked the cresta entirely in *Caduceia theobromae* (1937) and in the two species of *Pseudodevescovina* (1938). In the latter paper he illustrated the cresta of *C. theobromae* without comment, but in the earlier description he stated that the absence of the cresta (costule) characterizes *Caduceia.* The structure mentioned in *Pseudodevescovina punctata* as possibly a costule is actually something else, as will be explained later in this monograph.

I think it is possible that further study of the species of *Foaina* in *Neotermes aburiensis* will reveal a longer cresta and a parabasal body like that of *F. reflexa.* If that should be true, the name *F. reflexa* would probably become a synonym of *F. decipiens* (Grassé).

### **Foaina appendicula** sp. nov.

Plate 29, figures 50–51; figure C, 2

*Type host.*—*Glyptotermes minutus* Kemner. Ceylon.
T-313. (Cleveland. Collier.) (Syntype slide TP-264:2.)

*Diagnosis.*—Length 19 (9–32)μ; width 9 (4.5–17)μ; trailing flagellum a moderately stout cord at least twice the length of the body; cresta length 9 (5–11)μ; posterior part of parabasal filament extended to margin of body and posteriorly, parabasal body with a short ramus attached to the main part in the region near the posterior end of the nucleus; axostyle without enlarged cusp; nucleus 3.3 (2.8–4.4) × 2.8 (2.3–3.3)μ; long spirochaetes usually adherent over the entire surface of the body.

Very little material was available for study of this species, as only one slide had been prepared. Consequently, the technique used could not be sufficiently varied to make possible a complete account of the flagellate.

Of the parabasal apparatus only the chromophile part could be seen clearly, though the other substance was faintly visible in the Schaudinn–iron-haematoxylin preparations. The visible part of this substance began close to the posterior surface of the nucleus, where it was band-formed, and extended toward the periphery of the body, where it turned posteriorly. Apparently attached to this structure, in the region of contact with the posterior surface of the nucleus, was a short, deep-staining filament, representing an outgrowth or ramus of the parabasal apparatus (pl. 29, figs. 50, 51). In all specimens in which this ramus was observed it was single; but it is possible that there are sometimes additional outgrowths, overlooked in this instance because of the inadequacy of the material studied. In the early stages of division, of which a number have been seen, the parabasal body lacked the hook-formed appendage.

The flagellate has a yellowish appearance, owing to abundant wood fragments and other cytoplasmic inclusions, in contrast to that of *Devescovina arta* in the same preparations.

The small specimens, included in the minimum measurements in the diagnosis, are much like *Foaina nana,* except that many have adherent spirochaetes at the posterior end. The preparations were not suitable for study of the parabasal apparatus. These flagellates have not been separated from *F. appendicula,* in the absence of data sufficient to support such a procedure, but it is not unlikely that they really belong to different species.

## **Foaina duo** sp. nov.

Plate 29, figures 52–54; figure C, 3

*Type host.*—*Glyptotermes niger* Kemner. Java.

T-4543. Tapos. (Syntype slides TP-3218:16, 14, 13.)

*Diagnosis.*—Length 23 (17–28)μ; width 10 (6.5–13)μ; trailing flagellum moderately stout, stouter than the cresta for the posterior half or third of this, about twice the body length; cresta 11 (9–13)μ, slender; parabasal body with main part curved against the nuclear membrane, ending in a rather long free filament, short outgrowth at the posterior bend, in line with the transverse part of the proximal element, so as to form a bar that is met by the longitudinal part near its middle or one end; trunk of axostyle ending in a prominent, enlarged cusp, projecting often 6–11μ; nucleus 4.4 (3.3–6.6) × 2.3 (1.7–3.3)μ; no adherent microörganisms.

The parabasal apparatus (pl. 29, figs. 52–54) distinguishes this flagellate from all other devescovinids, but at the same time relates it to *Foaina hilli* (=*Crucinympha hilli*). The main part corresponds exactly to the corresponding part of the parabasal of that species (cf. fig. C, 3 and 4); it has the same type of anterior bend, diagonal longitudinal section, and transverse section near the posterior end of the nucleus ending in a rather long, posteriorly curved free filament. The outgrowth develops at the angle between the longitudinal and transverse sections of the main part, and appears continuous with the transverse section as a bar, just as in *F. hilli.* The somewhat oblique longitudinal section thus meets a transverse bar near its middle or toward one end, according to the length of the outgrowth. This length is never so great as that attained by the corresponding structure in *F. hilli.* Occasionally the outgrowth is absent altogether, and in some specimens it is no more than a knob. In one specimen (pl. 29, fig. 54) the end of the ramus was divided. No posterior outgrowth, like that completing the cruciform structure of the parabasal apparatus in some specimens of *F. hilli,* was observed in this species. Sometimes the shape of the parabasal resembles that of the numeral 2 (pl. 29, fig. 53); hence the specific name.

The parabasal filament separates from the longitudinal section of the main parabasal substance and approaches the anteromedial edge of the cresta (fig. C, 3). Thence it proceeds, as in other species, to join the blepharoplast; but this continuation to the blepharoplast, in contrast to the rest of the filament, is very delicate.

A clear collar-like structure appears around the enlarging part of the cusp of the axostyle within the cytoplasm. Anterior to the collar, spread more loosely around the trunk of the axostyle, is a ring of granules (fig. C, 3). The group varies in size and number of component granules, but its occurrence is constant. Often the group flares somewhat anteriorly.

The nucleus is elongated, with the two ends smoothly rounded and equal in size. The longer diameter is usually oblique, but not far from longitudinal, and the trunk of the axostyle meets the nucleus laterally, not at the end. There is no pointed prolongation of the nucleus along the trunk of the axostyle. In none of the preparations studied, which had been fixed in Hollande's, Flemming's, and Schaudinn's fluids, was any space present between the nuclear membrane and the chromatin mass. In the same preparations a marked space was present in all specimens of *Devescovina vestita.* The contents consisted of, besides the nucleolus, numerous uniform-sized granules. They appeared as discrete, rather large, deep-staining granules in certain material fixed in Hollande's fluid, and in general were larger and deeper-staining than in many species of *Foaina,* including *F. hilli.*

The absence of adherent microörganisms is in marked contrast to the abundance of spirochaetes on the associated flagellate *Devescovina vestita.* The latter flagellate bears spirochaetes and *Fusiformis*-like rods on all its surface except the most anterior part.

*Foaina duo* differs from *F. hilli* in its much smaller size, its longer cresta, and the prominent enlarged axostylar cusp, as well as in the less advanced development of the parabasal apparatus. Furthermore, numerous spirochaetes are always present on *F. hilli,* and rodlike microörganisms adhere to some specimens. All flagellates of the genus in *Glyptotermes niger* clearly belong to the one species; there is no smaller species comparable to *F. delicata,* which is associated with *F. hilli* in *Glyptotermes iridipennis.* This is significant, for if *F. delicata* were merely a "young stage" of *F. hilli* we might expect to find a comparable young stage of *F. duo.*

## **Foaina hilli** (Duboscq and Grassé)

Figure C, 4

*Devescovina hilli* Duboscq and Grassé, 1926, C. r. Soc. Biol., 94:33.—Duboscq and Grassé, 1927, Arch. Zool. exp. gén., 66:452, text figs. 1, 2, pl. 16, figs. 1–6.

*Crucinympha hilli* (Duboscq and Grassé) Kirby, 1938, Quart. Jour. Micr. Sci., 81:9, pl. 1, figs. 9–13.

*Type host.—Glyptotermes iridipennis* Froggatt. Australia.
T-304. (Hill.) (Xenosyntype slides TP-309:3, 2, 24.)
T-510. (Cleveland. Hill.) Barrington Top.N.S.W. (Xenosyntype slides TP-510:126, 79.)

*Additional hosts*
*Glyptotermes dubius* Mjoberg. Australia.
T-511. (Hill 3232.) Ravenshoe, Queensland. (Homosyntype slides TP-511:10, 49.)
*Glyptotermes perangustus* Hill. Australia.
T-512. (Cleveland. Hill.) Sydney. (Homosyntype slide TP-512:4.)

*Diagnosis.*—Length 35 (24–54; exceptionally, 69)μ; breadth 16 (11–24)μ; trailing flagellum a moderately stout cord; cresta length 7 (4.5–9.5)μ; trunk of axostyle stout anteriorly, tapering toward posterior end but not reduced to filament, sharpened end projecting from body, sometimes a little enlargement before projection, but no prominent enlarged cusp; capitulum moderately expanded; proximal element of parabasal apparatus curved against the nuclear membrane, continued in a free filament, one distal element attached at the posterior bend so that it forms a continuous bar with the transverse part of the proximal element, in many specimens a second distal element, often rather long, on the posterior side of this bar, completing a cross; nuclear axis oblique, chromatin fine, destaining readily, filling space within membrane, one or two nucleoli, size 5.5 (3.5–7) × 3.7 (2.6–5.3)μ; small spirochaetes, *Treponema hilli,* adherent over entire surface; often a tuft of longer spirochaetes on the papilla; *Fusiformis hilli* adherent in irregular grouping and variable number in some, but not in the majority of individuals.

Nothing can at present be added to the detailed descriptions of this flagellate by Duboscq and Grassé (1937) and Kirby (1938).

### **Foaina nucleoflexa** sp. nov.

Plate 29, figures 55–57; plate 30, figures 58–59; figures C, 5, E, 1–10

*Type host.—Cryptotermes merwei* Fuller. South Africa.
T-4048. Port Shepstone. (Syntype slides TP-2088:1, 10; 2089:2, 6.)

*Additional host.—Cryptotermes* sp. Tanganyika Territory.
T-1035b. Amani. (Homosyntype slides TP-1037b: 6, 7, 13.)

*Diagnosis.*—Length 37 (28–45)μ; width 14 (9–21)μ; trailing flagellum 60–80μ long, a stout cord in its middle part, reaching ½μ; cresta length 11 (9–13)μ; anteromedial edge about 1½μ, width decreasing at first abruptly, then gradually; parabasal body long, filamentous, most anterior part a section of moderate length beyond the blepharoplast, which is at the angle of this and the longitudinal part, followed by a U- or V-shaped section at one end of the nucleus, with its distal arm reaching close to anterior end of body, then a long filament, passing transversely and posteriorly, mostly anterior to the nucleus near the edges of the capitulum, one to seven short finger-like rami attached at the bend of the V or U; capitulum of axostyle a broad flat expansion, bearing short rodlike capitular granules; diameter of trunk of axostyle about 1μ, enlarged cusp projecting an unusual distance, 14–26μ, averaging 19μ; nucleus elongated transversely, and curved into an almost complete circle, like a stout-rimmed ring with a gap often of only 1 or 2μ, measurements of broadest side 5.6 (4.5–6) × 7.5 (7–9)μ; relatively long spirochaetes, usually about 10μ, adherent to anterior and posterior parts; also, on many specimens, filaments reaching 50μ.

*Foaina nucleoflexa* is the only species of the genus present in *Cryptotermes merwei.* It is one of the most advanced species of the genus, with its unusual nucleus, the long cusp, and the complex parabasal apparatus.

The three anterior flagella, with a length of 30–35μ, are about half the length of the trailing flagellum. They originate by roots adherent to the body along the prominent papilla, as is usual in Devescovininae. In fixed material they are distinctly separated from one another for all their free length.

The trailing flagellum begins as a slender filament which broadens as it passes along the cresta until at the distal end of this it has its greatest diameter, about ½μ. It continues at this size for a distance of a few microns, then narrows gradually to a filamentous distal end. It gives no evidence of being firmly adherent to the surface of the body above the cresta, often being entirely separated; but sometimes it parallels the cresta closely, even when the position of this is not the usual one.

In well-stained material the blepharoplast appears as a moderate-sized granule. In many specimens it is evident that this body is a group of several closely approximated granules. Outside of this group there are no accessory granules or rods, as in certain more advanced Devescovininae; and the anterior flagella run directly into the blepharoplast, with no enlargements of the roots.

The parabasal apparatus, although unusual, is essentially of the type in other species of *Foaina,* with the addition of appendages. The main parabasal body is a long structure of the *Foaina reflexa* type. Its proximal part passes posteriorly to a place along one side, about halfway between the anterior and posterior ends of the nucleus (pl. 30, fig. 58; fig. E). In no specimen observed did this longitudinal section extend as far posteriorly as the posterior end of the nucleus. At the region of the blepharoplast the anterior part of the parabasal turns sharply across the anterior surface of the nuclear membrane as a bar about 4μ long in some specimens (fig. E, 1–4; pl. 29, fig. 57). There is no enlargement at any point. The blepharoplast is situated at the sharp angle between this bar and the longitudinal part. At the posterior end of the short longitudinal part the parabasal bends anteriorly, continuing almost or quite to the level of the anterior edge of the capitulum (pl. 30, figs. 58–59). The chromophile filament then continues transversely and posteriorly around the anterior end of the body, close to the periphery, ending posteriorly at about the level of the nucleus (pl. 29, figs. 55, 56.)

When prepared by the Flemming-Regaud technique, the parabasal in the proximal part of the V and the anterior bar appears as a moderately stout, deep-staining rod. The distal part of the V appears double. One element is a deep-staining filament, which continues transversely and posteriorly as described above. The other part is stouter, runs parallel to the filament on the inner side of the limb of the V to its most anterior point, and then ends in a short, blunt hook. In the Flemming-Regaud material it is less well stained and less clearly defined than the proximal part of the apparatus. Its staining is, in fact, rather unusual for parabasal substance in Flemming-Regaud. This part is separated by a narrow, clear zone from the filament; nevertheless, there is no doubt that both are elements of one apparatus.

In the region of the bend of the V or U, alongside the nucleus, a number of short rami are attached (pl. 29, fig. 57; fig. E, 1–5). They suggest fingers or bananas attached to a loop. No specimen was observed without rami, though they are probably absent in early division material, which was not studied.

Some very short outgrowths are probably in an early state of development. In fifty specimens the number of rami ranged from one to eight, with distribution as follows: one, 2 specimens; two, 2; three, 10; four, 14; five, 11; six, 9; seven, 1; eight, 1. The average was 4.3.

Both the main part of the parabasal and the rami show the filamentous chromophile and the stouter chromophobe components in Flemming-Regaud material. In Schaudinn-Delafield material all parts of the parabasal except the terminal free filament are deeply stained and well defined. The long, fairly stout element along the filament from the loop to the anterior edge of the capitulum stains as deeply as other parts, and is therefore much better defined than in the Flemming-Regaud preparations used.

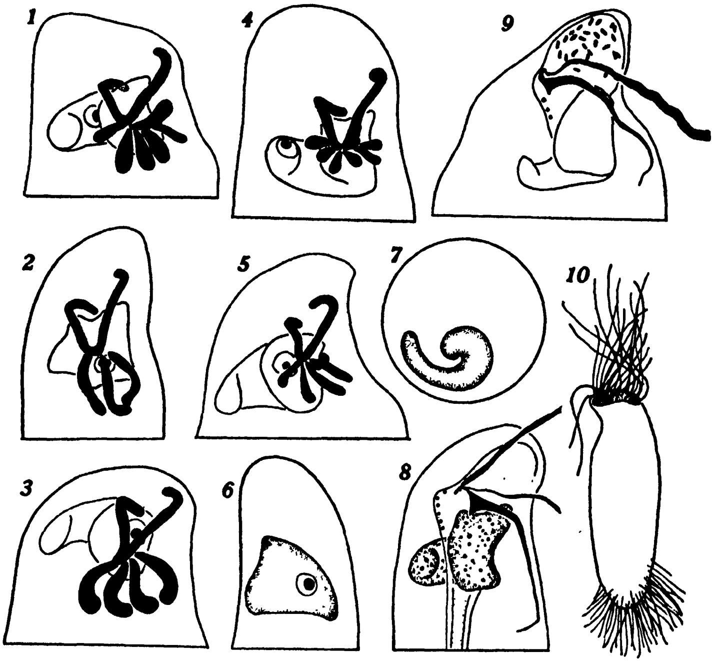

Fig. E. *Foaina nucleoflexa* sp. nov. from *Cryptotermes merwei*, South Africa. 1–5. Forms of the parabasal apparatus, with V-shaped main part and rami, ranging from 3 to 7 in number in these figures, attached near the point of the posterior bend. S.D. 6. Nucleus, viewed from the side in projection, showing triangular form. S.D. 7. Nucleus, viewed from anterior end, showing transverse elongation and curvature. S.D. 8. Diagram showing nucleus and mastigont structures, except the parabasal body; the axostyle does not pass within the curve of the nucleus, but lies outside it, above the broad part on the right. Fl.R. 9. Short rods on the capitulum. 10. Spirochaetes adherent to the anterior part of the body in a row along the surface above the parabasal filament, and to the posterior end. Fl.R. 1, 3–7, 9, × 1800; 2, 8, × 1750; 10, × 860.

The diameter of the trunk of the axostyle in the cytoplasm is about $1\mu$, without very much taper. At the posterior end it expands into a large spearhead-shaped cusp with a diameter of about $2\mu$ at its broadest part, which generally coincides with the end of the cytoplasm (pl. 30, fig. 58). The outlines of the broad part of the cusp are rounded, not sharp-angled like the cusps of some devescovinids. The sheath of the axostyle encloses a core which tapers gradually to the end. This is separated by a narrow space from the membrane in the trunk, but when the membrane expands in the cusp a much broader space is left.

The tapered end of the cusp is unusually long, extending beyond the cytoplasm for a distance equal to about half the length of the body. No specimens have been observed in which the projection of the axostyle was not great. In twenty specimens selected at random the projection ranged from 14 to 26μ. The greater part of this projection is a filament.

The trunk begins to expand into the capitulum at the posterior level of the nucleus. The boundary of the capitulum, as in all species, is an extension of the sheath of the axostyle, and is a thicker membrane than along the trunk. The core continues into the capitulum for a short distance, then disappears as such. The flare on one side is considerably greater than that on the other. The lesser flare brings the margin of the capitulum close to the blepharoplast; the flare on the other side brings the capitulum into the papilla. The wavy anterior margin of the capitulum runs parallel to the roots of the anterior flagella. Between the anterior edge of the body and the capitulum is a narrow zone of cytoplasm consisting of a clear region against the capitulum and a stainable region at the edge.

Short rods are present on the capitulum (fig. E, 9). Their number is variable. At one extreme there are only a few, perhaps none; generally the number is moderate, covering the capitulum sparsely; sometimes there are enough to cover it densely.

The nuclear structure is of the type usual in the genus, but the nucleus is unusual in its shape. The end near the cresta is the larger, often measuring about 6μ in a longitudinal direction (pl. 29, fig. 55). In a transverse direction the nucleus is greatly elongated, flattened, and curved (fig. E, 7). The outer edge of the part near the blepharoplast is straight or slightly concave (fig. E, 8); toward the other, narrower end it becomes convex. The diameter in the longitudinal direction of the flagellate decreases gradually to less than half of 6μ. The degree of curvature varies, but in most nuclei the circle is almost complete, a gap of only one or two microns separating the ends (pl. 29, figs. 55, 56). The nucleus is shaped like a doughnut, with a relatively small hole, about half as wide on one side as on the other, and with a small piece cut out on one side. The axostyle does not pass through this open ring; the posterior part of the capitulum is located outside it, against the broadest part of the nucleus (pl. 30, fig. 59).

The cytoplasm contains many pieces of wood which range in size from very small up to more than half the length of the body. Several pieces of moderate relative size are present in most individuals. There are also numerous cytoplasmic granules. A narrow peripheral zone is free of coarse inclusions.

All specimens have spirochaetes adherent to the anterior and posterior parts (fig. E, 10), though scattered ones are often present on the middle part of the body. Most of these spirochaetes have distinct spiral forms and a length of about 10μ. Many of those on the anterior end are arranged in a row along the surface above the parabasal filament. Adherent to many specimens are some straight, filament-formed organisms ranging in length from about 10 to 50$\mu$, but generally of the greater length. This is probably a different organism from the spirochaete. The shorter filaments are stouter than the spirochaetes and lack the spiral shape.

### **Foaina ramulosa** sp. nov.

Plate 30, figures 60–66; figure C, 6

*Type host.*—*Cryptotermes* sp. nov. Madagascar.
T-4403. Near Tulear. (Syntype slides TP-3151:12, 2, 6.)

*Diagnosis.*—Length 48 (20–66)$\mu$; width 25 (11–40)$\mu$; trailing flagellum a stout cord, length 55–80$\mu$; cresta slender, length 15 (11–18)$\mu$, anteromedial edge 1$\mu$ or less; parabasal apparatus compound, with a recurved main part, extended in a free filament, from which arises a distal ramus often with one, two, or three branches, occasionally with outgrowths from the branches as well as from the ramus itself; capitulum expanded, extended considerably beyond the limit of the nucleus anteriorly, thickly encrusted with deep-staining granules and short rods; trunk of axostyle moderately stout, with no enlarged cusp, projecting for a length of 10–20$\mu$, sometimes more; nucleus ellipsoidal, 7 (3.5–8) × 5 (2.5–6)$\mu$; no adherent microörganisms.

*Foaina ramulosa* was comparatively infrequent on the smears studied, being far less abundant than *Devescovina glabra* or either of the other two species of *Foaina*. As it was believed at the time of collection that the host belonged to the same species as certain other *Cryptotermes* that had been collected, and as no difference in the flagellates had been noted, only a few preparations were made. This limitation in material available for study makes it necessary to give a description that is in part incomplete.

The organelles of the mastigont meet anteriorly at a compact blepharoplast. Near this there sometimes seems to be another granule, or an irregular substance prolonged posteriorly from the blepharoplast proper. The blepharoplast was seen, however, in only a few specimens, and then indistinctly, so this interpretation of the organization is tentative.

The cresta narrows rapidly from the anteromedial edge, and for the greater part of its length it is a very narrow band as seen from the surface, and little more than a filament as seen from the side (pl. 30, fig. 65). The flat side of the band is parallel to the surface of the body; and sometimes in Schaudinn–iron-haematoxylin preparations it appears for part of its length as a double line, only the edges staining.

The trailing flagellum is very slender for a distance of 4 or 5$\mu$, then it thickens rapidly to a stout cord. When cresta and trailing flagellum are viewed from the aspect in which the two appear separately and parallel to one another, the flagellum is considerably stouter than the cresta for most of the length of the latter.

The parabasal apparatus consists of a main part and a ramus that is usually branched. The main part often has the outline of a sickle, with the handle a deep-staining filament (fig. C, 6). The chromophile substance at the deepest part of the curve is a band, broadened to the full width of the structure.

The parabasal structure described above is the whole of the parabasal apparatus in a number of small-sized individuals (pl. 30, fig. 64). Outgrowths of it are present, however, in most specimens. In its simplest form the outgrowth is a single bar, arising near the middle part of the main substance (pl. 30, figs. 60, 62, 65). When this outgrowth is fully developed its length exceeds that of the Delafield-staining part of the main parabasal structure (fig. 62). The bar usually has a curvature in the reverse direction to that of the other substance; but its form is somewhat irregular. In most specimens there are one, two, or sometimes three outgrowths from this bar (pl. 30, figs. 61, 63). These vary in length and in position along the bar. Outgrowths may occur not only from the bar itself, but from these branches; but no more than one short outgrowth of a branch has been seen in a single specimen. In Schaudinn-Heidenhain preparations a deep-staining filament along one edge of the bar and each of its branches may be demonstrated.

The trunk of the axostyle, after extending straight through the body, projects in a long, sharpened spike (pl. 30, fig. 65). In the absence of an enlarged cusp, the species is markedly unlike *Foaina hamata* in the same material, which has a very large cusp. The trunk abuts against the nucleus at one side. Before this point is reached, however, the outer membrane of the axostyle spreads out dorsally to form the dorsal part of the capitulum.

The capitulum (pl. 30, fig. 66) is broad and sharply outlined. From one aspect it has a bluntly pointed, spatulate form, extending anteriorly considerably beyond the limits of the nucleus. Viewed from the side, it appears flattened and extends at an angle to the longitudinal axis of the body, bending dorsally. Ventral to the capitulum, between it and the edge of the body, is a clear area. The anterior part of the capitulum is thickly incrusted with deep-staining granules and short rods.

The nucleus is ellipsoidal, elongated in a transverse direction, and has one large, spherical, deep-staining peripheral nucleolus. There is no clear space under the nuclear membrane; and the chromatin mass is composed of small densely packed granules. The nucleus is a rounded structure, with no indication of the flattened, curved form of that of *F. nucleoflexa,* or of the grooved form characteristic of some devescovinids of this group.

The cytoplasm usually contains numerous fragments of wood and a great many granules, so that it is dense in appearance. There is a narrow, clearer zone at the periphery.

The small-sized individuals of *Foaina ramulosa* resemble the accompanying, more numerous species, *F. hamata.* By critical observation, however, it is not difficult to distinguish the two. They are similar in size, shape, and trailing flagella. The anterior part of the body of *F. ramulosa* is prolonged into more of a point, and the capitular extension into this region is much more sharply outlined. The prominence of the capitulum is due in large part to the thick incrustation of deep-staining granules. Another marked difference is the large cusp in one species and the complete lack of this in the other. The cresta of *F. ramulosa* is usually 13–18$\mu$ long, whereas that of *F. hamata* is 7–9$\mu$. There is also a difference in the form of the parabasal body, even when only the main part of that of *F. ramulosa* is present.

## **Foaina pectinata** sp. nov.

Plate 31, figures 67–73; figure C, 7

*Type host.*—*Anacanthotermes ochraceus* Burmeister. Egypt.
T-1007. Sharkiya Province. (Syntype slides TP-1012:16; 1020:8.)

*Diagnosis.*—Length 37 (23–47)μ; width 19 (10–31)μ; trailing flagellum little stouter than an anterior flagellum, not longer than body; cresta in form of a section of a slender thorn, length 4(3–5)μ; main part of parabasal sickle-formed, with a moderately long portion on the side of the blepharoplast opposite from the rest; parabasal usually with 1–5 rami grown out along the main part, the first outgrowth often close to the blepharoplast; axostyle with expanded capitulum and moderately stout trunk, sharpened projecting cusp usually moderately enlarged; nuclear diameter 5.1 (4.5–6)μ; usually scattered spirochaetes, often 5–6μ long, adherent over entire surface of body.

Duboscq, Grassé, and Rose (1937) made no mention of this flagellate in their brief account of the protozoa of *Anacanthotermes ochraceus* in Algeria. In most preparations that I have studied it is not abundant.

The flagellate stands somewhat apart from other species of *Foaina.* The trailing flagellum is slender and its length, 40–54μ in some specimens, does not very much exceed the length of the body. In this relatively short and slender trailing flagellum it differs from typical members of the genus. There is a short trailing flagellum in *Pseudodevescovina.* In the table I prepared (1937*a*) I listed a species of *Pseudodevescovina* from the Hodotermitidae; *Foaina pectinata* was the flagellate referred to.

The main part of the parabasal body is curved against or near the nuclear membrane and has a rather long continuation beyond the region of closest contact with the blepharoplast (pl. 31, figs. 67, 68, 70). This anterior section is longer than in any devescovinid I have studied except *Parajoenia grassii.* In a few smaller individuals (pl. 31, figs. 67, 70) the parabasal is unbranched, but most specimens have from one to five outgrowths attached to the main part (pl. 31, figs. 68, 69, 71). Often there is such a ramus not far from the blepharoplast (pl. 31, fig. 69), but frequently the rami occur only in the posterior portion (pl. 31, fig. 68). There is much variation in the number and length of the outgrowths. Some are mere buds; others are comparatively long. Evidently the rami elongate during the vegetative life of the flagellate. It may be that from time to time parts of the parabasal are cast off and resorbed in the cytoplasm.

Over the entire surface of most individuals there are scattered spirochaetes (pl. 31, fig. 73), many of which have a length of 5 or 6μ. They often are particularly abundant at the posterior end.

Ingested bodies of various kinds, including fragments of vegetable matter, are sometimes present in the cytoplasm; but most specimens examined enclosed little or no foreign material. A parasite resembling *Sphaerita* is frequently present (pl. 31, fig. 72).

## GENUS PARAJOENIA JANICKI

### **Parajoenia** Janicki

*Parajoenia* Janicki, 1911, Biol. Centralbl., 31:324 (type species *P. grassii* Janicki).—Janicki, 1915, Zeitschr. wiss. Zool., 112:594.—Kirby, 1937, Univ. Calif. Publ. Zoöl., 41:220.

*Diagnosis.*—Size moderately large, rounded anteriorly and posteriorly, papilla not conspicuous; three long slender anterior flagella; one long trailing flagellum; cresta of moderate size; parabasal apparatus highly developed, single, consisting of a long, two-angled main part and often one or more rami arising at the posterior bend, anterior bend close to the blepharoplast; stout axostyle with pointed posterior end projecting a short distance from body, expanded anteriorly, beginning posterior to nucleus, into a very large leaflike capitulum bearing a longitudinal keel; nucleus relatively small in size, with longer axis oblique or transverse, no clear space under membrane, chromatin granules small, one or more peripheral nucleoli.

### **Parajoenia grassii** Janicki

Figure F, 1–3

*Parajoenia grassii* Janicki, 1911, Biol. Centralbl., 31:324, fig. 3.—Janicki, 1915, Zeitschr. wiss. Zool., 112:586, pl. 14, figs. 18, 22, text figs. 3–6.—Kirby, 1937, Univ. Calif. Publ. Zoöl., 41:215, pl. 13, figs. 1–8, text fig. A.

*Type host.*—*Neotermes connexus* Snyder. Hawaiian Islands.
T-307. (Adamson.) Kahaniki, Oahu. (Xenosyntype slides TP-306:1, 3.)
T-306. (Fulloway.) (Xenosyntype slide TP-208:9.)

*Diagnosis.*—Length 45 (29–59)μ; width 24 (12–33)μ; stout cordlike trailing flagellum about 0.3μ maximum width, often 1½ times body length; cresta length 9 (7.5–11; exceptionally, 14)μ; anterior section of parabasal V-shaped, with apex close to blepharoplast, posterior section beyond posterior bend passing anteriorly, transversely and obliquely, equal in length to the anterior section, short ramus present at the posterior bend, continuous with the posterior limb of the V; trunk of axostyle stout, posterior end sharpened without preceding enlargement and projecting a short distance; capitulum broad with a high, narrow longitudinal ridge or keel; nucleus 5.6 (5–6.3) × 3 (2.3–3.4)μ; no adherent *Fusiformis*-like rods; numerous spirochaetes, about 15–20μ long, adherent to anterior and posterior parts of body; peripheral cytoplasm of posterior part of body containing ellipsoidal bodies that show a spatial relationship to the ends of the attached spirochaetes.

I recently (1937*b*) published a description of this flagellate, in which the account by Janicki (1915) was corrected, supplemented, and reinterpreted. In the following year Grassé recognized the assignment of *Parajoenia* to a position among the polymastigote flagellates and stated his opinion that *Foaina* is a synonym of *Parajoenia*. He thought it probable, furthermore, that *P. grassii* and *F. gracilis* are actually one species. He based this opinion, in part, on his conception of the structure of *"Parajoenia" decipiens,* which I have previously discussed (1938*b*; and this paper, p. 210). It is necessary to give a further discussion here of the relationship of *Parajoenia* and *Foaina.*

Although I have been unable to obtain any of Janicki's original preparations, I have been able to study excellent preparations of *P. grassii* and *F. gracilis* from the same termite species that provided his material. I think there is no reason to doubt that the two flagellates are independent species.

They are, of course, the type species of the genera *Parajoenia* and *Foaina,* and a study of their relationship is crucial in connection with the question of the independence of the genera. The genus *Foaina* contains many species; the genus *Parajoenia,* one. *Parajoenia* has priority over *Foaina,* and if there is no independence the name *Parajoenia* must be used for a large group of these typical polymastigote flagellates.

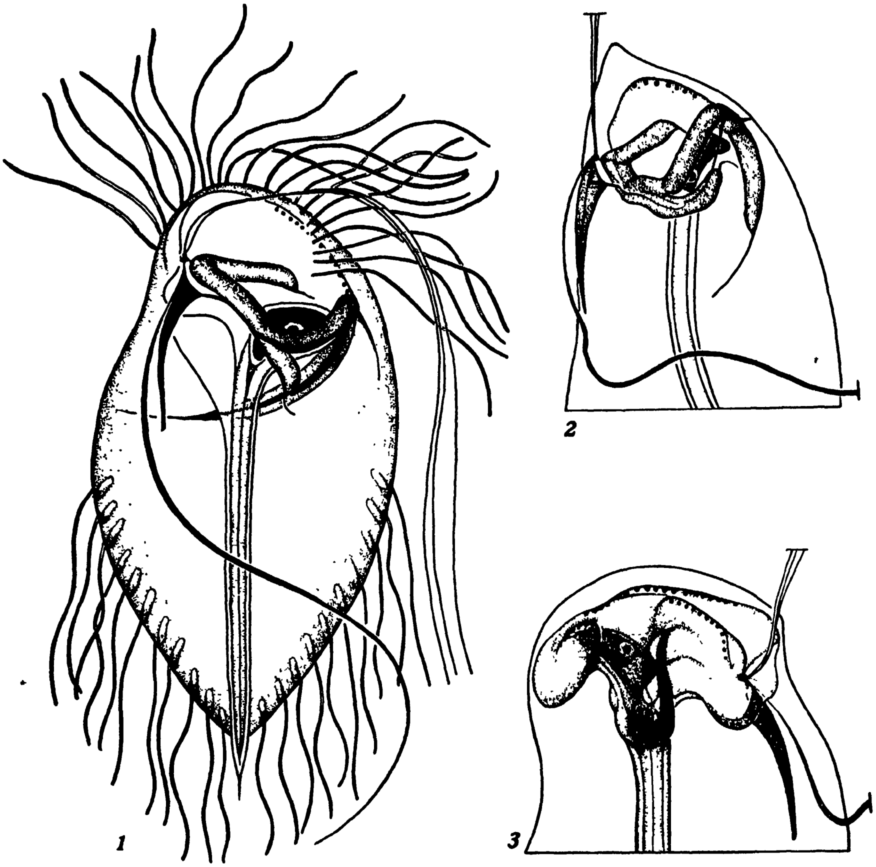

Fig. F. *Parajoenia grassii* Janicki from *Neotermes connexus,* Hawaii. × 1750. 1. Some of the spirochaetes adherent to the anterior and posterior parts of the body are shown. Those of the posterior part have a spatial relationship to ellipsoidal structures, in the peripheral cytoplasm, which are shown only in optical section of the outermost edges. The capitulum is very broadly expanded in the anterior part of the body. The main part of the single parabasal apparatus begins in the V-shaped structure near the blepharoplast, then bends sharply and continues in a curved element that here passes under the axostyle. At the sharp bend there arises a short outgrowth or ramus. 2. Diagram showing the parabasal body and the relationship of the filament that separates from the anterior part of this to the cresta. This filament, instead of extending straight to the blepharoplast, meets a filament that extends longitudinally along the cresta. 3. Diagram showing capitulum, as seen from the left side. In the center part, extending toward the observer, is the high, narrow ridge; the trunk of the axostyle, in this diagram, extends posteriorly from the region of the ridge.

There are no differences of value for generic distinction between *Foaina* and *Parajoenia* in flagella and cresta. The dimensions of *P. grassii* could be included within the considerable range of size in the genus *Foaina*. There are four features only on which generic independence can be supported, and these are of debatable value. They are the axostyle, the parabasal apparatus, the nucleus, and the ellipsoidal bodies in the peripheral cytoplasm.

The parabasal apparatus is highly developed, but it is essentially of the type in the genus *Foaina*. The parts of the apparatus (fig. F, 1, 2) were not correctly identified in my earlier account. The main part includes the part there designated as the distal element, and most of the proximal element. This main part begins as a V-shaped structure whose apex is close to the blepharoplast; then, near the posterior part of the nucleus, it bends at approximately a right angle and continues in a long curved structure. It has much similarity in form to the parabasal apparatus of *Foaina reflexa*. At the posterior bend there originates in most specimens a short outgrowth; sometimes there are two of these. There is a difference from most species of *Foaina*, and other devescovinids too, in that the first part of the parabasal is not applied to the nuclear membrane; but there is a similar separation in *Foaina nucleoflexa*. If, therefore, the parabasal apparatus is to be used in generic definition, it is only the degree of its development that is significant.

In *Parajoenia grassii* the trunk of the axostyle is unusually stout and there is a greatly expanded, keel-bearing capitulum. The axostylar capitulum has undergone considerable expansion in certain species of *Foaina*. In *Foaina* this expansion does not begin far posterior to the nucleus, as in *P. grassii;* but this is related to the unusually small nuclear size in *P. grassii*. As genera of Devescovininae are defined in this paper, there are considerable differences among congeneric species in the form and the degree of expansion of the capitulum. Nevertheless, the great enlargement of the structure in *P. grassii* relative to the size of the nucleus, the beginning of the expansion posterior to the nucleus, and the unique keel, may be regarded as significant, in connection with other points.

The nucleus of *Parajoenia grassii* is relatively very small in size. Its dimensions are comparable to those of the nucleus of *Foaina falcifera;* but the length and breadth of the body of *P. grassii* average more than twice those measurements in *F. falcifera*.

The rather large ellipsoidal bodies in the posterior peripheral cytoplasm (fig. F, 1) of *P. grassii* are unique, so far as I have observed, in Devescovininae. The spatial relationship to adherent spirochaetes which they seem to show (Kirby, 1937*b*) is not understood. There are intracytoplasmic bodies related to surface structures in *Foaina signata*. In any case, the ellipsoidal bodies are not mastigont structures and their value for taxonomy of generic order is doubtful.

Grassé (1938) mentioned the absence of spirochaetes from the *Foaina* studied by Janicki, in contrast to their presence on *Parajoenia*. He was of the opinion that spirochaetes may have been present on *F. gracilis*, but were overlooked or had been lost in the course of technical manipulation. My observations support Janicki in regard to their absence from *F. gracilis*. The point, however, is not-significant; congeneric species of Devescovininae, and sometimes even individuals within a species, may differ from one another in the presence of adherent spirochaetes.

If the two genera were united, it would not be on the basis of the points advanced by Grassé; for he lacked a complete and accurate understanding of the structure of either of the type species. His main point, apparently, was the supposed presence of two parabasal bodies in both, although I pointed out the incorrectness of this concept, as far as *Parajoenia* is concerned, in the paper (1937*b*) which Grassé cited in another connection.

Although no unequivocal decision on the matter can be made, it has seemed to me best to continue to list *Parajoenia* and *Foaina* as separate genera. A situation that is similar in many respects exists in the genera *Devescovina* and *Caduceia.* A basis for this decision can be found in the relatively very small size of the nucleus in *Parajoenia;* in the great expansion of the capitulum, the beginning of this rather far posterior to the nucleus, and the presence of the longitudinal keel; and in the advanced development of the parabasal apparatus—all these points considered together.

It should be pointed out that the orientation given to *P. grassii* in my 1937 description is not in agreement with that adopted in these studies of Devescovininae. The side on which the blepharoplast is situated was then called ventral; in the present descriptions, following customary usage, that side is designated as dorsal. The capitular expansion of the axostyle is thus on the left, not the right, side of the nucleus; and the high, narrow ridge arises from the left side of the capitulum (fig. F, 3).

The chromophile element of the parabasal apparatus is well defined along the distal part of the structure and the ramus, and it continues as a free filament beyond the end of each of these parts. Before the blepharoplast is reached, the chromophile filament separates from the other substance of the parabasal and passes along the surface of the cresta, passing the angle between the anteromedial and posteromedial edges (fig. F, 1, 2). On the surface of the cresta it meets at a right angle a filament that comes from the blepharoplast, and from this point a filament oftens seems to continue along the cresta.

## SUMMARY

Descriptions are given of 26 species of *Foaina* Janicki. Of these, 19 are new: *F. acontophora, F. appendicula, F. costata, F. duo, F. exempta, F. falcifera, F. funifera, F. hamata, F. humilis, F. minuscula, F. nucleoflexa, F. ovata, F. parvula, F. pectinata, F. ramulosa, F. reflexa, F. signata, F. solita, F. taeniola.* Of the remaining names, 5 are new combinations: *F. decipiens* (Grassé), *F. dogieli* (Duboscq and Grassé), *F. grassii* (Duboscq and Grassé), *F. hilli* (Duboscq and Grassé), and *F. nana* (Kirby).

All except *F. pectinata,* which stands somewhat apart from the other species, occur only in termites of the large former genus *Kalotermes* sensu lato. Flagellates of the genus are present in all but 39 of the 132 species of these termites that I have examined, and are indicated in published reports of 2 other species that I have not seen. Forty-four hosts have one species, 42 have two, and 3 have three; the other 4 have at least one. *F. pectinata* occurs in *Anacanthotermes ochraceus.*

*Janickiella* Duboscq and Grassé, *Paradevescovina* Kirby, and *Crucinympha* Kirby are synonyms of *Foaina* Janicki. *Janickiella duboscqi* de Mello, from a lizard, is not a devescovinid flagellate. Probably it belongs to the genus *Monocercomonas.*

The genus *Foaina* includes the smallest Devescovininae, but some species are of moderate size. The cresta is narrow, and ranges in length, in different species, from very short to the full length of the body. The trailing flagellum is generally much longer than the body. In most species it is cordlike, but occasionally it is flattened or ribbon-formed. The end of the axostyle projects from the body, with an enlarged cusp or not with one. The capitulum ranges from a simple expansion to a broadened, curved membrane. The parabasal body is not turned around the axostyle. In most species it is a single, simple body, but in several there are rami in characteristic form and arrangement. There are no longitudinally adherent rods; adherent spirochaetes are present or not present.

The genus *Parajoenia* Janicki is closely related to *Foaina.* Its retention here as a separate genus (instead of reduction of *Foaina* to synonymy with it) is based upon a number of characteristics considered together. These are the relatively very small size of the nucleus, the greater expansion of the capitulum, the beginning of this rather far posterior to the nucleus, the presence of the longitudinal keel of the capitulum, and the advanced development of the parabasal apparatus. The only known species is *P. grassii* Janicki. *P. decipiens* Grassé is removed to the genus *Foaina.*

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## LITERATURE CITED

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# PLATES

All figures have been drawn with the aid of the camera lucida.

Abbreviations for methods of preparation: B., Bouin's fluid; C., Champy's fluid; D., Delafield's haematoxylin; E., eosin., Er., erythrosin; F., acid fuchsin; Fl., Flemming's fluid; H., iron-haematoxylin; Holl., Hollande's fluid; Os.V., osmic vapor; R., Regaud's haematoxylin; S., Schaudinn's fluid.

# PLATE 23

All figures × 2400.

Figs. 1–3. *Foaina grassii* Duboscq and Grassé from *Kalotermes flavicollis.* 1, 2, Os.V.H.; 3, B.H.

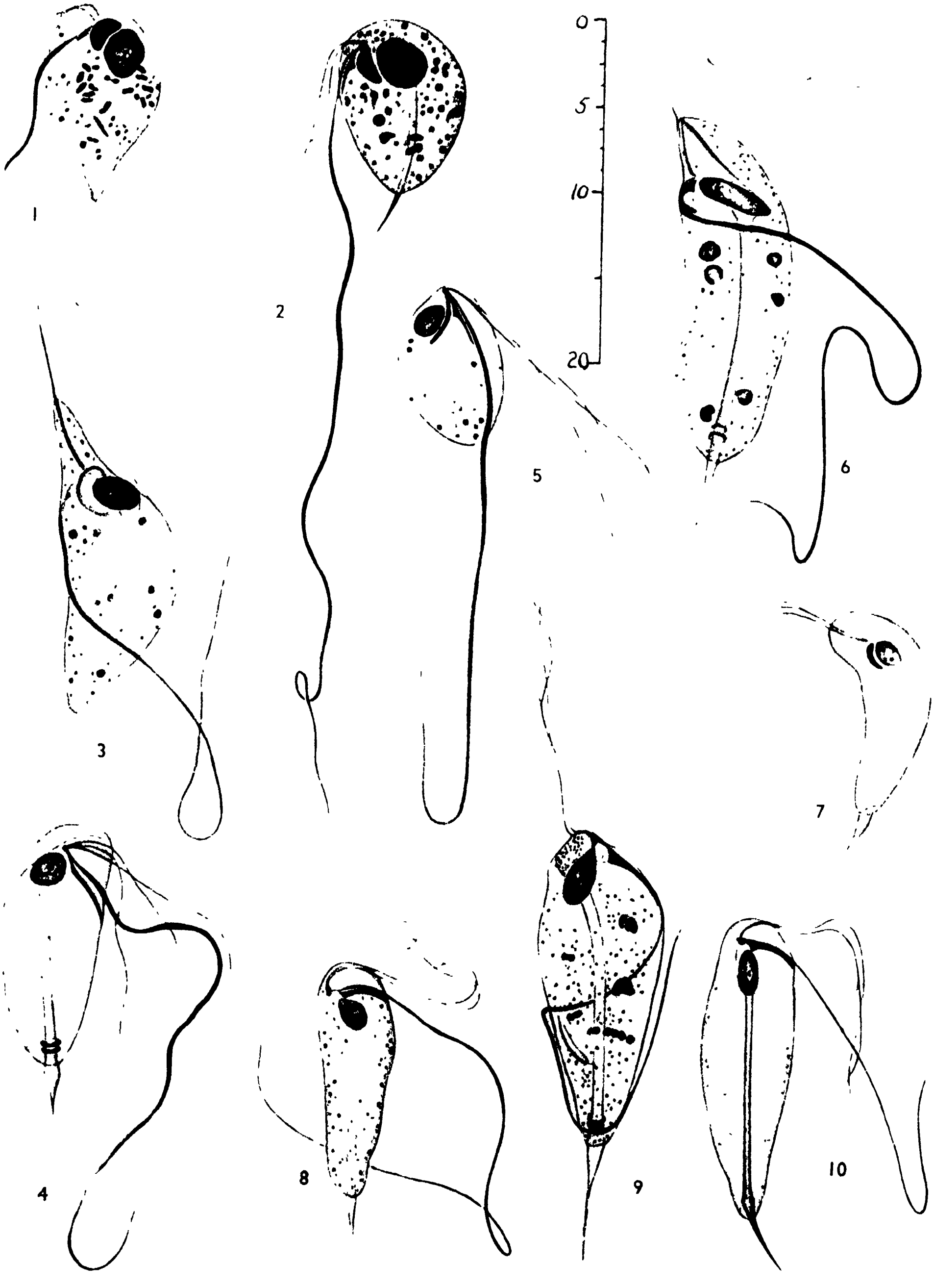
Figs. 4–9. *Foaina solita* sp. nov.

Figs. 4–5. From *Cryptotermes dudleyi.* 4, S.H.E.; 5, Os.V.H.

Figs. 6–8. From *Rugitermes kirbyi.* 6, 8, S.H.; 7, S.D.

Fig. 9. From *Glyptotermes parvulus.*

Fig. 10. *Foaina parvula* sp. nov. from *Glyptotermes contracticornis.* S.H.



## PLATE 24

All figures × 2400.

Figs. 11–12. *Foaina humilis* sp. nov. from *Cryptotermes brevis.* 11, S.D.; 12, S.H.

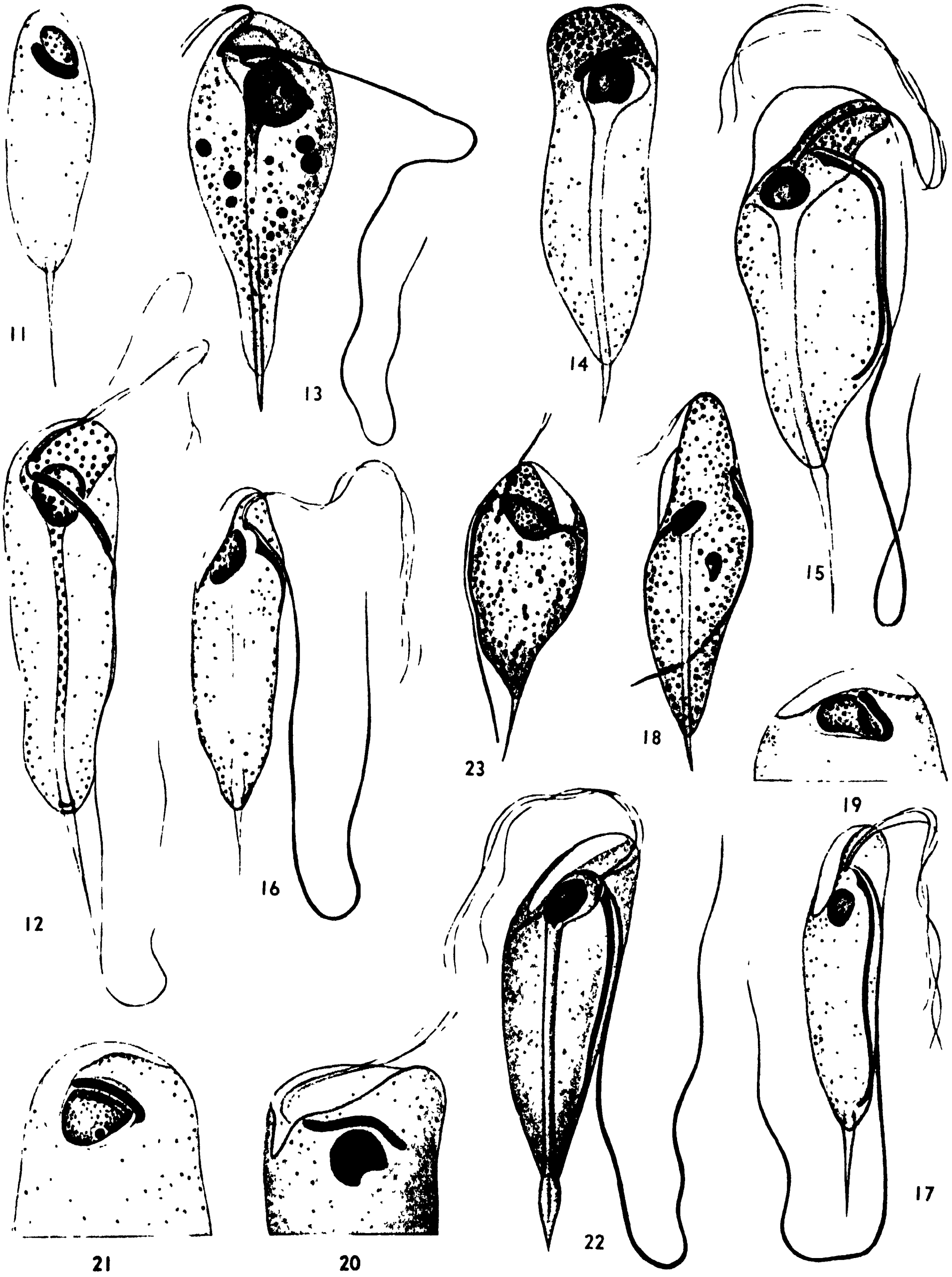
Fig. 13. *Foaina exempta* sp. nov. from *Neotermes insularis.* S.H.

Figs. 14–23. *Foaina nana* Kirby.

Figs. 14–20. From *Rugitermes kirbyi.* 14, 19, 20, S.D.; others S.H.

Fig. 21. From *Rugitermes panamae.* S.D.

Figs. 22–23. From *Cryptotermes dudleyi.* 22, S.H.; 23, Fl.H.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## PLATE 25

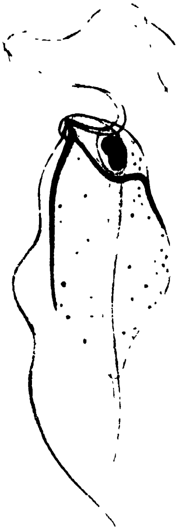
All figures × 2400.

Fig. 24. *Foaina nana* Kirby from *Cryptotermes hermsi.* S.H.

Fig. 25. *Foaina nana* Kirby from *Cryptotermes* sp., Java, possibly *C. dudleyi.* C.R.

Figs. 26–29. *Foaina costata* sp. nov. from *Neotermes insularis.* 26, Fl.R.; others, S.H.

Figs. 30–31. *Foaina dogieli* (Duboscq and Grassé) from *Kalotermes flavicollis.* B.H.



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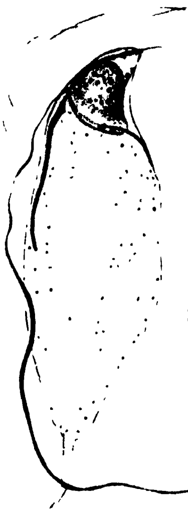

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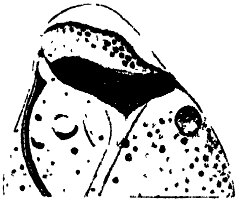

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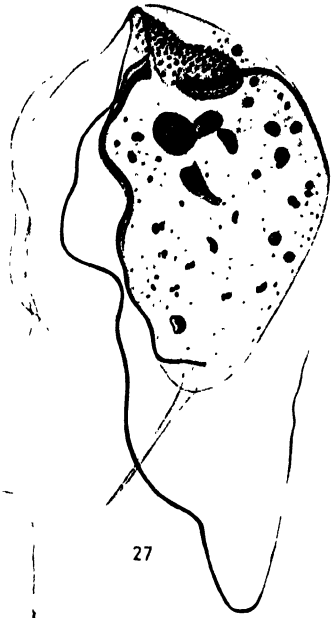

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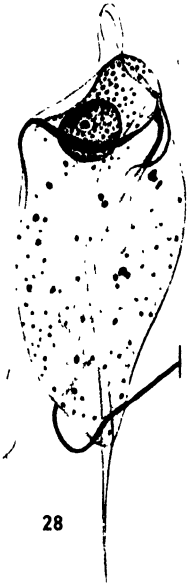

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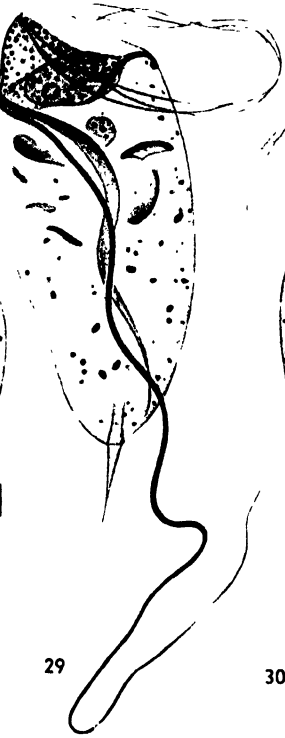

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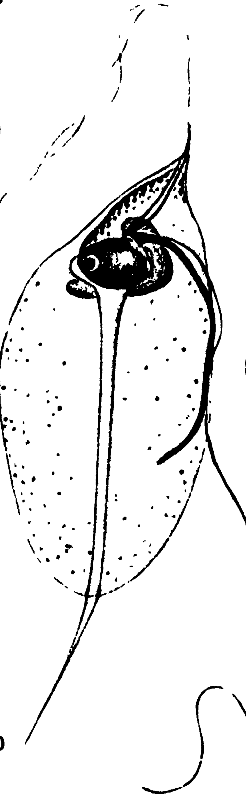

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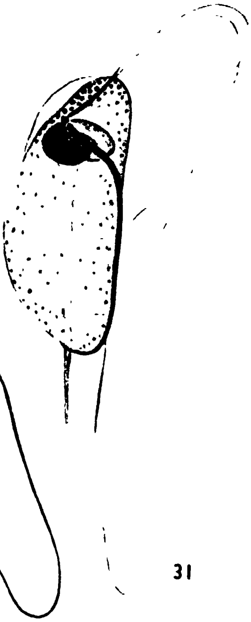

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## PLATE 26

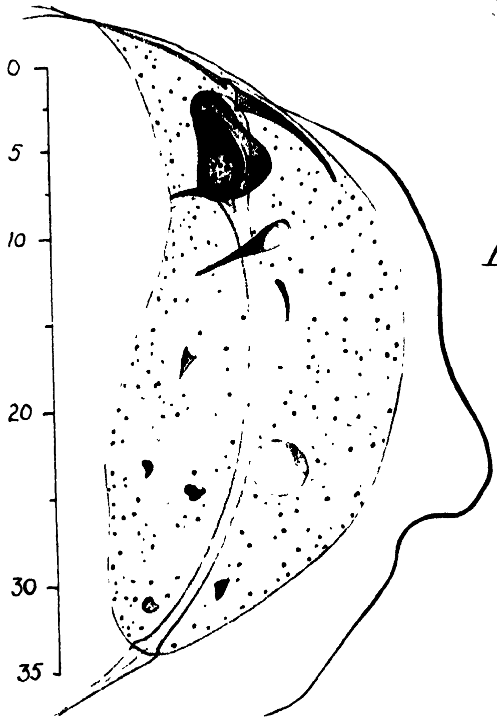
Figs. 32–33. *Foaina hamata* sp. nov. from *Glyptotermes parvulus*. ?H. × 2400.

Fig. 34. *Foaina delicata* Kirby from *Glyptotermes dubius*. S.H. × 2334.

Fig. 35. *Foaina acontophora* sp. nov. from *Cryptotermes* sp. T-3092. S.H. × 2334.

Fig. 36, *a–f*. *Foaina signata* sp. nov. from *Kalotermes* sp. T-3025. Nuclei showing peripheral nucleolus (2 nucleoli in *a*) and large body with 5 or 6 deep-staining granules. S.H. × 2334.

Scale × 2400.



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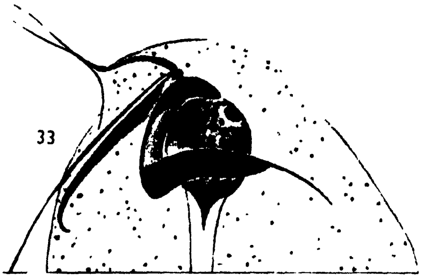

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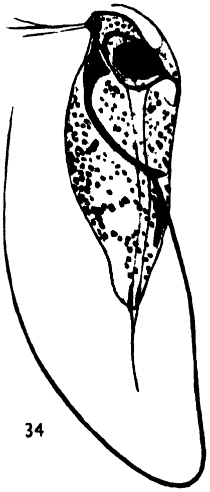

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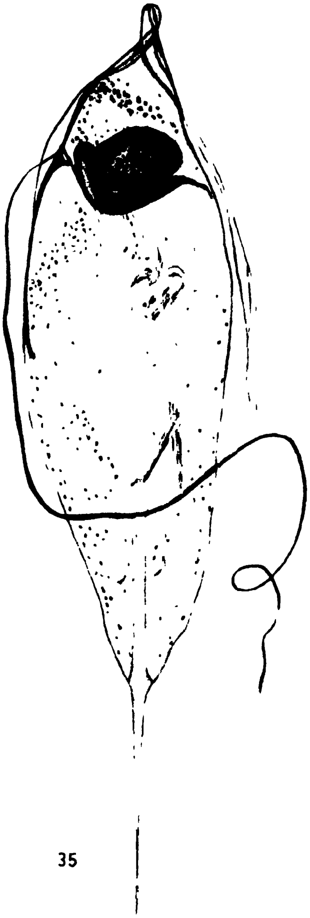

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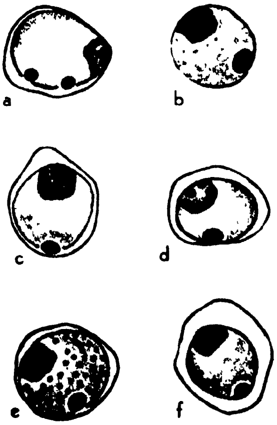

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## PLATE 27

Figs. 37–38. *Foaina signata* sp. nov. S.D. × 2334.

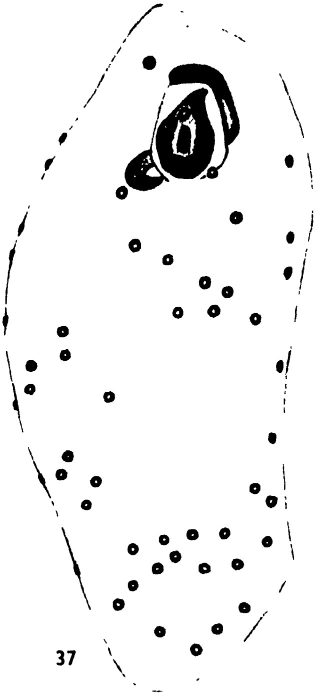
Fig. 37. From *Kalotermes* sp. T-3025. Disc-shaped bodies adadherent to surface.

Fig. 38. From *Neotermes meruensis.* Surface discs fewer and larger, with substance extended in cytoplasm below.

Figs. 39–43. *Foaina falcifera* sp. nov.

Figs. 39–41. From *Glyptotermes contracticornis.* 39, 41, S.H.; 40, S.D. × 2400.

Figs. 42–43. From *Glyptotermes montanus.* 42, S.H., × 1767; 43, C.R., × 2400.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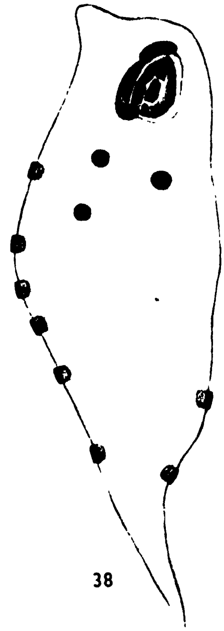
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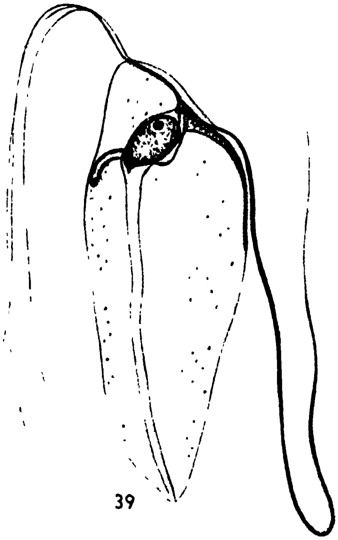
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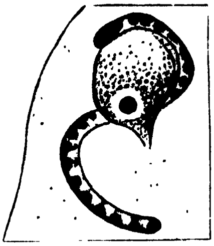
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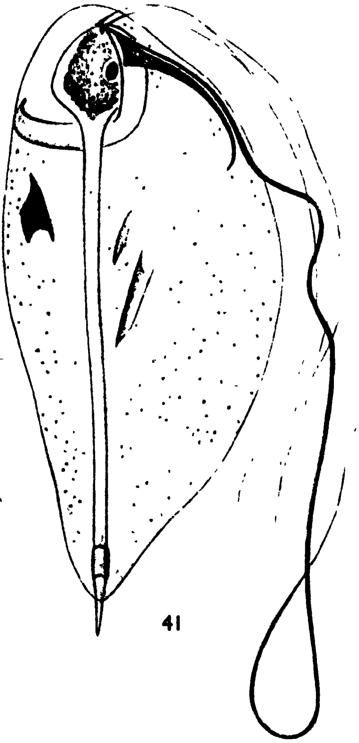
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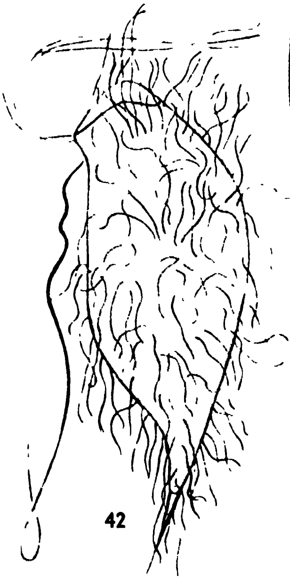
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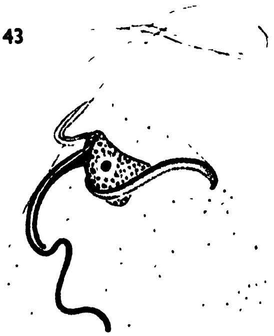
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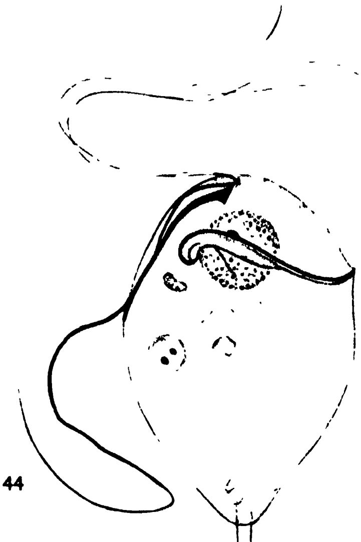
## PLATE 28

*Foaina reflexa* sp. nov.

Figs. 44–46. From *Kalotermes perezi.* 44, 45, S.II.; 46, S.D. × 2400.

Figs. 47–48. From *Cryptotermes longicollis.* S.H. Er. × 2400.

Fig. 49. From *Neotermes castaneus.* Chromophile band of parabasal body, and frilled attachment. Fixation Hollande, stained in protargol. × 2334.



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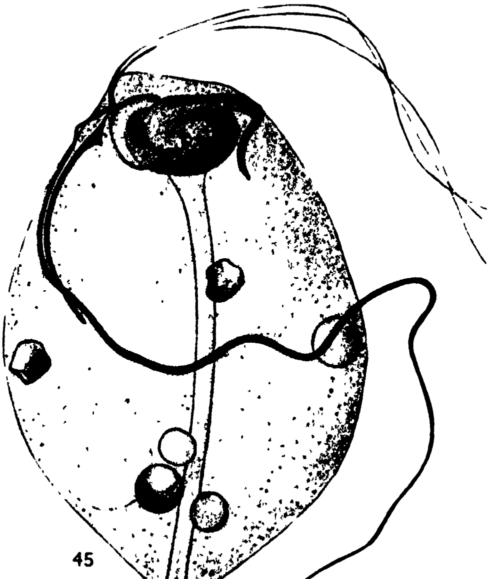

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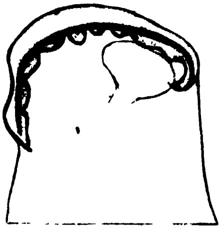

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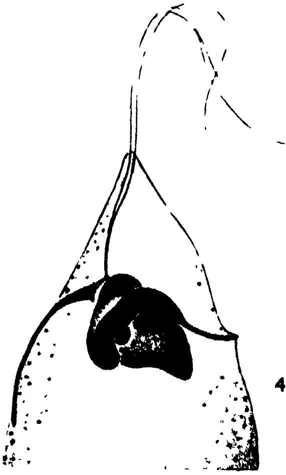

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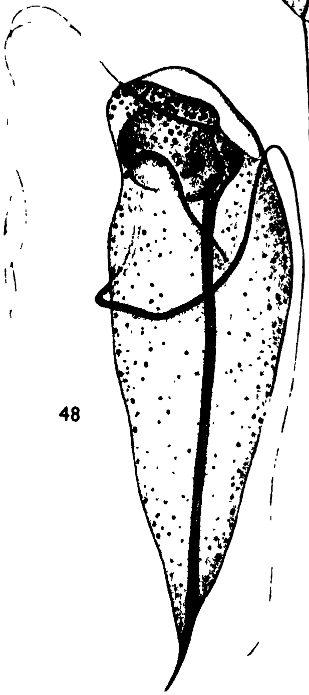

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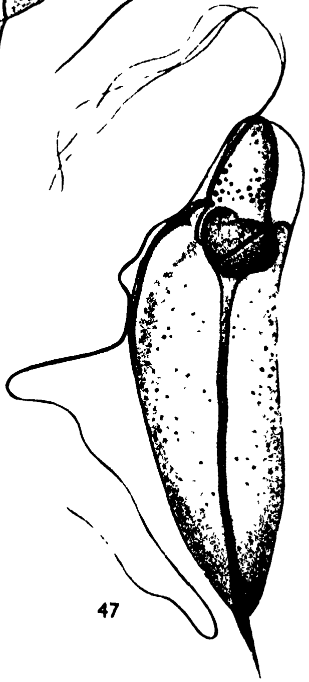

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## PLATE 29

Figs. 50–51. *Foaina appendicula* sp. nov. from *Glyptotermes minutus*. The shorter filament in the parabasal apparatus represents the outgrowth. Not all the parabasal is visible in these preparations. S.H. × 2400.

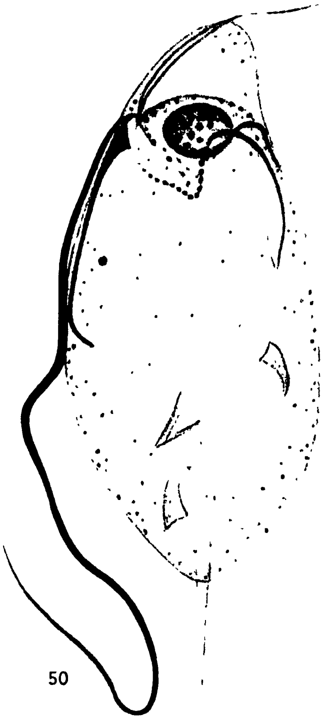
Figs. 52–54. *Foaina duo* sp. nov. from *Glyptotermes niger*. Forms of the parabasal apparatus, showing single outgrowth from the main part, which is curved in close contact with the nucleus. In 54 the outgrowth is branched. S.D. × 2334.

Figs. 55–57. *Foaina nucleoflexa* from *Cryptotermes merwei*.

Figs. 55–56. Curved form of nucleus, anterior to which the edge of the capitulum appears as a heavy fibril. Outside this, passing posteriorly, then turning anteriorly and passing around the anterior part of the body, is the parabasal filament. S.H. × 2334.

Fig. 57. Complete parabasal apparatus, with group of outgrowths attached at the posterior bend. The parabasal filament continues transversely beyond the end of the stouter substance, to the opposite side of the body anterior to the nucleus. Fl.R. × 2334.

Scale × 2334.



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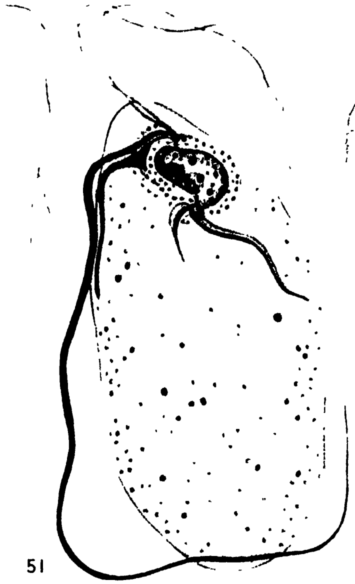

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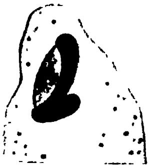

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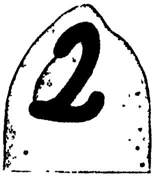

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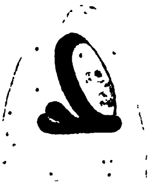

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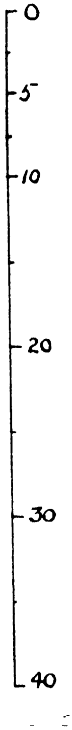

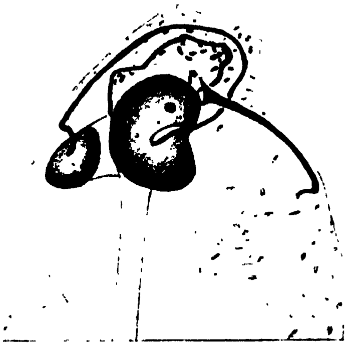

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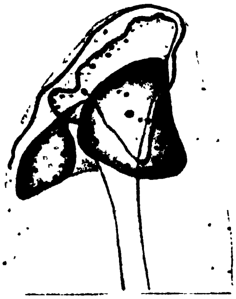

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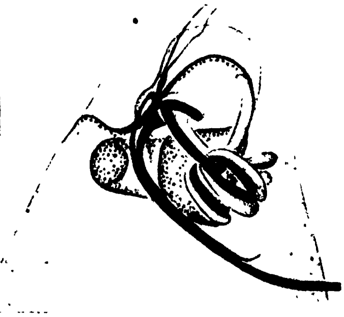

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# PLATE 30

All figures × 2334.

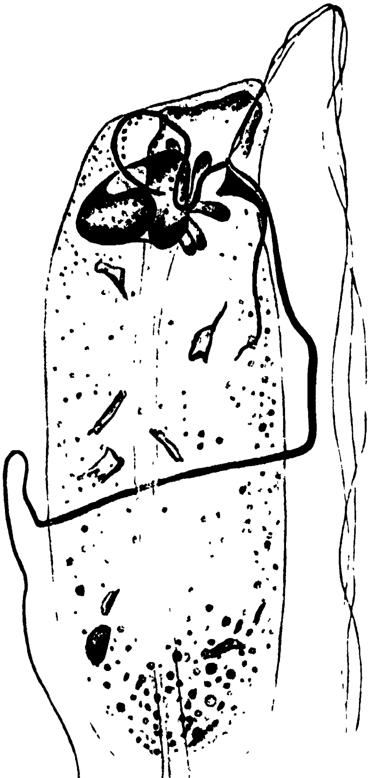
Figs. 58–59. *Foaina nucleoflexa* sp. nov. from *Cryptotermes merwei.* Curvature of nucleus, trunk and capitulum of axostyle, parabasal filament in sigmoid form, group of parabasal appendages in 58. 58, Fl.R.; 59, S.H.

Figs. 60–66. *Foaina ramulosa* sp. nov. from *Cryptotermes* sp. nov. T-4403.

Figs. 60–64. Forms of the parabasal body, with various types of outgrowths except in 64, where no outgrowth is present. 60, 61, 63, S.D.; 62, 64, Fl.R.

Fig. 65. Entire. Parabasal with single, unbranched outgrowth extended posteriorly. Fl.R.

Fig. 66. Ellipsoidal nucleus and capitulum of axostyle; ends of parabasal structures. Fl.R.



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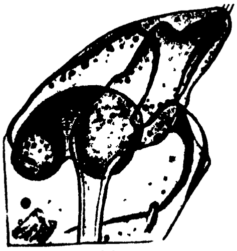

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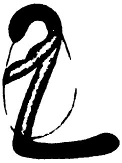

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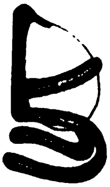

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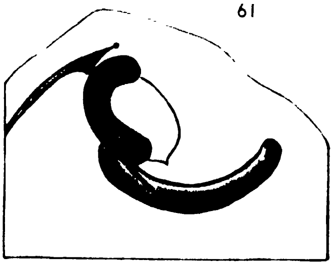

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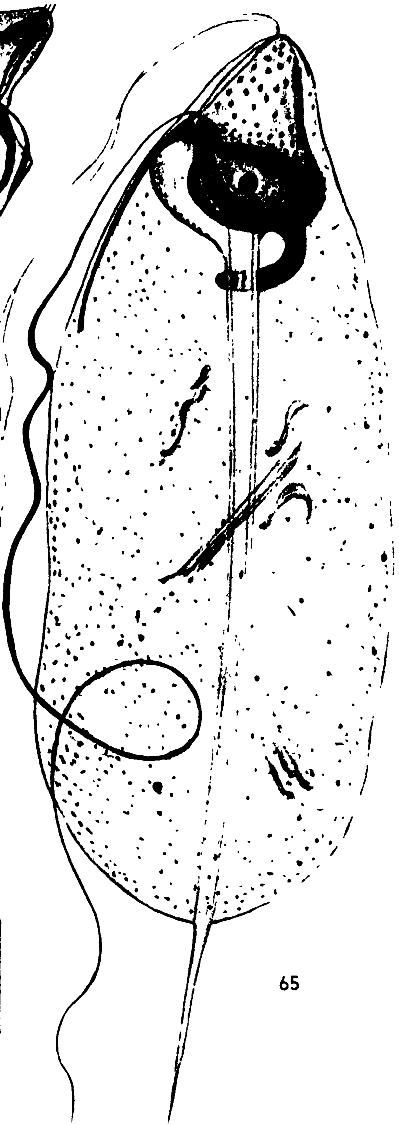

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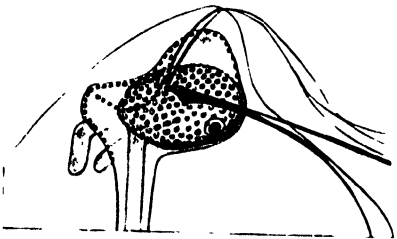

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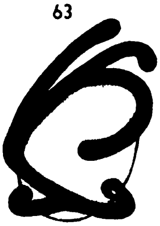

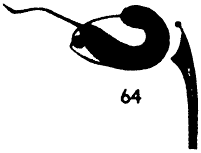

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## PLATE 31

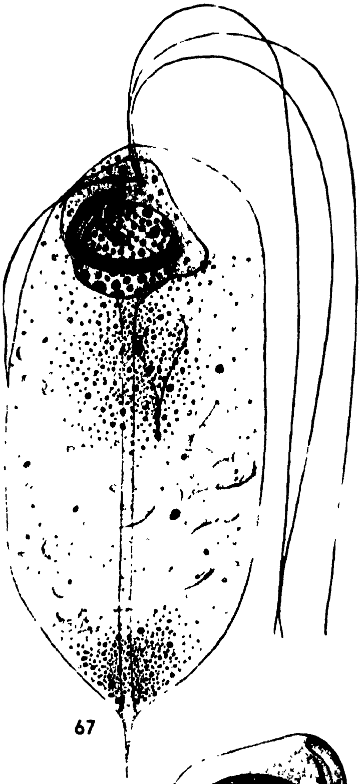
*Foaina pectinata* sp. nov. from *Anacanthotermes ochraceus.*
S.H. Fig. 73, × 1334; others, × 2334.

Fig. 67. Entire; unbranched parabasal body, broad capitulum; trailing flagellum slender, about length of body.

Figs. 68–71. Parabasal body, unbranched in 70, has rami at various points along main limb in the others.

Fig. 72. Large inclusions in cytoplasm, including a sporangium of a *Sphaerita*-like parasite.

Fig. 73. Spirochaetes adherent to surface.



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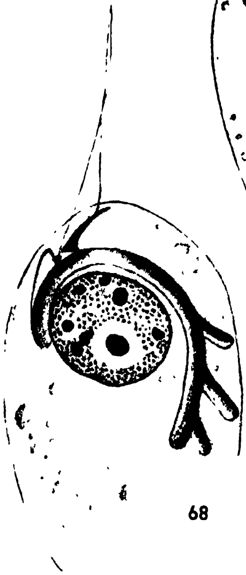

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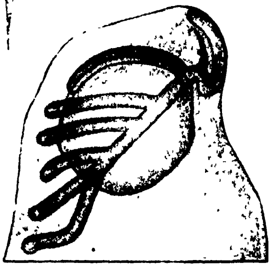

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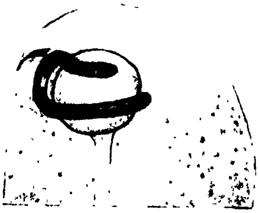

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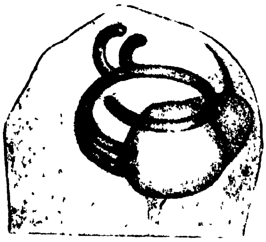

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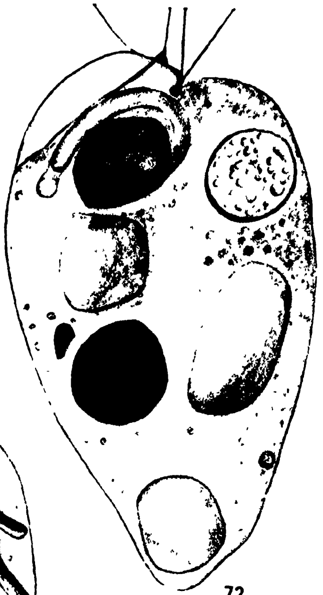

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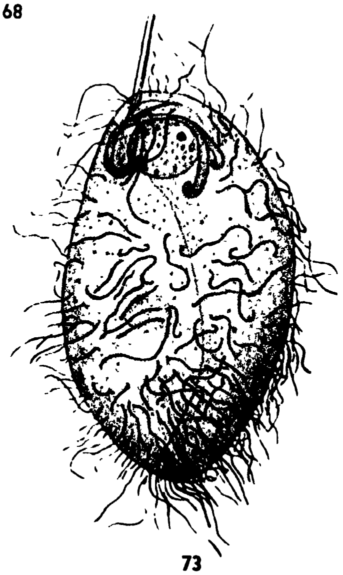

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# DEVESCOVINID FLAGELLATES OF TERMITES

# IV. THE GENERA METADEVESCOVINA AND PSEUDODEVESCOVINA

BY

HAROLD KIRBY

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4 MAY 1949

# DEVESCOVINID FLAGELLATES OF TERMITES
# IV. THE GENERA METADEVESCOVINA AND PSEUDODEVESCOVINA

BY

HAROLD KIRBY

## DESCRIPTIVE AND SYSTEMATIC ACCOUNT

### GENUS METADEVESCOVINA LIGHT

### **Metadevescovina** Light

*Metadevescovina* Light, 1926, Univ. Calif. Publ. Zoöl., 29:141 (type species *M. debilis* Light).—De Mello, 1941, Proc. Ind. Acad. Sci. (B), 14: 83.

*Diagnosis.*—Body usually stout in form; size moderate to large, average length 21–70μ, range 9.5–90μ; average width 8–29μ, range 4–41μ; three long anterior flagella; trailing flagellum usually cordlike, occasionally flattened or ribbon-like, about as long as the body to twice this; cresta variable in length, average from about 4μ to 24μ, greatest length 32μ; parabasal body spiraled around the axostyle from less than 1 turn to 7 turns, usually simple, occasionally branched in posterior part, no free posterior parabasal filament; trunk of axostyle relatively stout to end of cytoplasm, enlarged cusp present in some species, typically always some projection from posterior end of cytosome, length ranging from very little to more than that of the body; capitulum simple in some species, but often developed more or less in membranous extensions; position and structure of nucleus similar to that of *Foaina;* some species with no adherent microörganisms, but most with spirochaetes on the posterior end, often also on the anterior end, and sometimes on the whole surface of the body.

## TAXONOMY AND DISTRIBUTION

Of the sixteen species included in this paper, three have already been described. *Metadevescovina debilis* Light is the type of the genus. *M. stereociliata* and *M. polyspira* were originally put into the genus *Devescovina* by Grassi (1917) and Lewis (1933), respectively, but, as explained in the accounts of the species, I have found reason to change the generic assignment. In listing the protozoa of *Kalotermes minor* in 1934, I published the name of a fourth species, *M. cuspidata*, as *M. cuspidis;* and a figure was given without a description.

Light separated *Metadevescovina* from *Devescovina* on the basis of several characteristics, among which was the supposed presence of a number of short tertiary flagella in addition to the usual flagellar equipment. Duboscq and Grassé (1927), believing it possible that these were spirochaetes, suggested that perhaps *Metadevescovina* should be placed in synonymy with *Devescovina*. In 1938 Grassé concluded on the basis of his observations on other devescovinids that these were spirochaetes, as I had stated in 1937. De Mello (1941), in his summary of the characteristics of species and genera of Devescovinidae, included the presence of short flagella in the diagnosis of *Metadevescovina*. He had, however, merely accepted the statements in Light's paper; and he made no reference in this connection to the other publications cited above.

Light stated (1926, p. 155): "Aside from the presence of tertiary flagella, *Metadevescovina* differs from *Devescovina* in the peculiar shape and position of its nucleus and in the complicated internal membrane and lamella and the accompanying clear areas. In the absence of the tertiaries these would place it in a separate but closely related genus." My observations have led me to support this opinion, with certain departures from the reasons given. The nucleus, both in its internal structure and in its shape and position, differs considerably in *Metadevescovina debilis* and in species of *Devescovina*. In some other species of *Metadevescovina* the difference is less notable. The elaborate structure of the capitulum of the axostyle, to which Light actually refers in his second reason, is characteristic of several but not of all species of *Metadevescovina*. A significant difference from *Devescovina* exists in the trunk of the axostyle, which is slender, tapering, and enclosed in the cytoplasm in *Devescovina*, but is generally stout and projects posteriorly in *Metadevescovina*. A fact that aids in distinguishing the two genera, although it is not strictly of taxonomic value, is the uniform presence of striations (bacteria) on *Devescovina*, and the absence of this characteristic type of striation on *Metadevescovina*.

The sixteen species of *Metadevescovina* occur in twenty hosts, only one of which, *Mastotermes darwiniensis*, does not belong in the Kalotermitidae. Five times as many species of Kalotermitidae have been found to lack *Metadevescovina*; the genus is much less frequent than *Foaina* and *Devescovina*. Only two hosts, *K. marginipennis* and *K. jouteli*, have more than one species each. Host limitation is marked. Twelve of the species have one host each. Two of the others occur in closely related hosts, of the same genus, in the same general region: *M. stereociliata* occurs in two species of *Glyptotermes* in tropical Africa, and the flagellate faunule is essentially the same in both of these; *M. nitida* occurs in two species of *Procryptotermes* in Madagascar, both in the same region; the termites are closely related and have the same flagellate faunule. Another species, *M. fulleri*, occurs in several species of *Kalotermes* in South Africa and Madagascar; in all of them the faunule is similar if not identical. An exception appears in certain colonies of termites that contain *M. fulleri*, and which have been assigned to *Kalotermes madagascariensis* by Emerson. These colonies have the expected type of faunule, but that of other colonies assigned to the same species is different (p. 269).

Two noteworthy facts in the distribution of *Metadevescovina* deserve mention. *Devescovina* has only once, in *Glyptotermes angustus*, been found in the same host as *Metadevescovina*, and *Foaina* is seldom present. The only instances of association with *Foaina* are in *Glyptotermes parvulus* and two new species of *Glyptotermes*, all of tropical Africa. The fact of the usual absence of association with *Foaina* is important in opposition to the opinion that certain *Foaina*-forms may be developmental stages of other devescovinids.

## GENERAL MORPHOLOGY

The body of species of *Metadevescovina* is stout, in comparison with that of *Devescovina*, the average width often being about half, more or less, of the length, and at least being more than a third; in *Devescovina* the average width is most frequently less than a third, and only in the one species *D. vittata* is it almost as much as half of the length. In *Metadevescovina* the posterior part is usually more rounded than in the typical *Devescovina* with its tapering, pointed end.

The blepharoplast group consists of several granules which in most species are aggregated into a compact structure; often the group appears as a single large granule. Granules sufficiently separated to be individually recognizable can be seen in *M. debilis* (pl. 41, fig. 61), as noted by Light (1926), and in *M. fulleri* (pl. 40, fig. 53). In the latter species there is a separate flagellar granule at the end of one of the flagellar roots, connected by a filament to the blepharoplast (fig. E, 1). The slender rhizoplast that connects the blepharoplast to the nuclear membrane has been observed in several species, and probably occurs in all.

Although the cresta varies greatly in length in different species, it is rather constant in both relative length and shape within a species. It has a typical devescovinid form in most species. The cresta of *M. carina* (pl. 40, fig. 54, fig. D) and *M. nitida* (pl. 41, fig. 60) is broadened in the direction of the anteromedial edge for a large part of its length, so that the breadth often exceeds the length of that edge.

The principal difference between *Metadevescovina* and *Foaina* is in the type of parabasal body. It is turned around the axostyle in the former genus, but not, whatever its length, in the latter. In *Foaina* the parabasal filament is often continued free for a certain distance beyond the distal end of the parabasal body, but no free filament has been seen in *Metadevescovina.* In most species of *Metadevescovina* the proximal end of the parabasal body extends beyond the blepharoplast on the anterior surface of the nucleus, with the parabasal filament separating and extending directly to the blepharoplast (pl. 35, fig. 22). In *M. debilis,* however, the whole parabasal, both filament and body, passes directly toward the blepharoplast, and the parabasal body terminates in a rounded end a short distance before reaching the granule.

In the length of the parabasal body, and in consequence the number of turns, there is much diversity in different species. The spiral sometimes is looser and more open than it ever is in *Devescovina*; but some species have as close a spiral as do most members of that genus. Outgrowth of a branch of the parabasal body takes place occasionally in several species (*M. cuspidata, M. debilis, M. fulleri*); in rare instances there are two or three rami. In *M. polyspira* several rami occur in practically all large specimens (fig. C, 4).

Heterogeneity in the substance of the parabasal body, which consists of blocks or granules of Delafield-staining or silver-impregnating substance alternating with clear areas, or of clear vesicles in the stainable substance, is a marked characteristic of some species of *Metadevescovina* (pl. 42, figs. 67, 68). I discussed (1931) this feature in the structure of the parabasal body of *M. cuspidata* and *M. debilis.* It is important to note that the flagellate then referred to as *Devescovina* sp. from *Kalotermes minor* is actually *Metadevescovina,* because similar heterogeneity has been observed in no species of *Devescovina.*

A feature of *Metadevescovina* is the elaborate development of the capitulum of the axostyle in some species. A similar development occurs in *Devescovina insolita,* but has been seen in no other species of that genus. Capitula that in simplicity are like those of most species of *Devescovina* occur in *M. modica, M. stereociliata, M. carina,* and other species. There is a restricted development of a membranous extension in *M. cuspidata* and *M. cristata.* The membranous extension is large, turns around the nucleus, and forms a trough that contains the anterior part of the parabasal in *M. debilis* (pl. 41, fig. 63), *M. fulleri* (pl. 39, fig. 52), and *M. nitida* (pl. 41, fig. 60). In *M. magna* the membrane turns in a still longer spiral, with the parabasal body, however, inside (pl. 43, fig. 76).

Granules are often present on certain areas of the capitulum. A chromatic shield of typical form was found in *M. nitida,* and probably occurs also in other species.

The trunk of the axostyle resembles that of *Foaina*. It generally is stout, and is of moderately decreasing diameter from a short distance posterior to the nucleus to the end of the body, where it may or may not be enlarged. In typical specimens there is always a projecting part of a length that varies within a species and among species. Certain species, such as *M. debilis*, characteristically have a short projection (pl. 41, fig. 61), whereas it is moderately long in *M. stereociliata* (pl. 35, fig. 21) and other species. Its length equals or exceeds that of the body in *M. nudula* (pl. 39, fig. 49). Light (1926) called attention to the fact that in *M. debilis* the axostyle may project for a length nearly equal to the body in degenerating specimens. In the reports in this paper I have taken care to avoid degenerating or abnormal individuals, and have been concerned with only the normal projection of the axostyle.

Although reference has been made in earlier papers to the *Metadevescovina* type of nucleus, as distinct from the type in *Devescovina*, study of additional material has shown more variability among species of the genus than was then supposed to exist. There are nuclei in certain species of the genus that are scarcely different from some in *Devescovina*. In general, however, there are marked differences. Whereas in *Devescovina* the nucleus is usually regularly ellipsoidal or ovoidal in form, in *Metadevescovina* it is frequently more elongated or irregular in outline. A posterior nuclear extension along the trunk of the axostyle occurs in some species but not in others. In several species the nucleus is extended posteriorly at one side of this pointed projection, with a consequent groove or concavity in it. There is some development of this in *M. modica* and *M. cuspidata*, and it is carried so far in *M. cristata*, *M. turbula*, and *M. patula* that the nucleus has as a whole a marked curvature (pl. 38, fig. 42). There are often also other irregularities and angularities in outline. In *M. debilis* and *M. magna* elongation is pronounced; there is a neck extended toward the blepharoplast. The longer axis usually is in an oblique direction, but sometimes it is almost transverse.

Between the central chromatin mass and the membrane a clear zone, so frequent in *Devescovina*, is usually lacking, as in *Foaina*, but it occurs often enough so that its absence cannot be given as a generic characteristic. No clear zone has been observed in any material of the nuclei of most species, and in other species it was observed in some preparations but not in others. When present in some specimens, it was often absent from others on the same slide. There is no species of *Metadevescovina* in which the occurrence of a marked clear zone, as in many species of *Devescovina*, is a universal characteristic in my preparations. Whether the result of shrinkage or not, this nuclear structure is less frequent and less marked in the former genus.

The internal structure of the nucleus is usually like that typical of *Foaina*, with one or two deep-staining peripheral nucleoli and granular chromatin that destains more readily. Large deep-staining granules and masses of material, like those characteristic of *Devescovina*, occur in the chromatic mass of some specimens of many species, however, so that the nucleus as a whole appears more deeply stained. Both types of nuclei have been observed in different preparations of the same species, and there are all degrees of intergradation.

On the surface of the body there generally are present no rods of the *Fusiformis* type that constitute "striations" on all species of *Devescovina*. Some are present, however, on many specimens of the small flagellates assigned to *M. polyspira* (pl. 42, fig. 72), though they seem to be lacking on the larger ones typical of the species.

Adherent spirochaetes are absent from *M. extranea*, *M. carina*, *M. nudula*, and *M. modesta*. Some species have a group of spirochaetes on the posterior part of the body only, but usually there is also a tuft on a region near the anterior end. In some species (*M. modica*, *M. debilis*, *M. magna*) spirochaetes always cover the entire surface of the body (pl. 43, fig. 75); and in *M. fulleri* they either cover the body or are restricted to the anterior and posterior parts (pl. 39, figs. 50, 51).

## KEY TO THE SPECIES OF METADEVESCOVINA

1. Average length of cresta under 7μ .......... 12
   Average length of cresta more than 7μ .......... 2
2. Parabasal body with several branches in almost all large individuals .......... *M. polyspira*
   Parabasal body rarely branched .......... 3
3. Parabasal in a close spiral usually of 3–4 turns, up to 7 .......... *M. modesta*
   Parabasal spiral averaging less than 2 turns .......... 4
4. Trailing flagellum bandlike .......... *M. stereociliata*
   Trailing flagellum cordlike .......... 5
5. Breadth of cresta for much of its length equaling or exceeding the anteromedial edge .......... 6
   Cresta tapering, of more typical form .......... 7
6. Parabasal body usually with not more than 1 turn; capitular extension moderate; gap present in parabasal substance .......... *M. carina*
   Parabasal body with 1 to 2½ turns; capitulum elaborately extended; usually no gap in parabasal substance .......... *M. nitida*
7. Nucleus elongated obliquely or transversely and markedly curved .......... 8
   Nucleus not so elongated and curved .......... 10
8. Cresta usually more than 20μ in length .......... *M. cristata*
   Cresta usually less than 15μ in length .......... 9
9. Maximum length of cresta not more than 10μ .......... *M. turbula*
   Minimum length of cresta more than 10μ .......... *M. patula*
10. Projection of axostyle equaling or exceeding length of body .......... *M. nudula*
    Projection of axostyle generally less than half the length of the body .......... 11
11. Capitulum elaborately extended; nucleus ellipsoidal .......... *M. fulleri*
    Capitulum moderately extended; nucleus often angular and with a lateroposterior extension .......... *M. cuspidata*
12. Average length about 25μ; trunk of axostyle relatively slender .......... 13
    Average length more than 30μ; trunk of axostyle a relatively stout rod .......... 14
13. Capitulum simple; parabasal body with longitudinal section and part on anterior surface of nucleus; cresta more than 5μ long .......... *M. mediocris*
    Capitulum expanded; parabasal body extended diagonally posteriorly from blepharoplast in an unbroken spiral; cresta less than 5μ long .......... *M. extranea*
14. Capitulum of axostyle simple .......... *M. modica*
    Capitulum of axostyle with large membranous extension .......... 15
15. Membranous extension of capitulum narrow and long, anterior part of parabasal body internal to membrane .......... *M. magna*
    Membranous extension broader, anterior part of parabasal in trough external to membrane .......... *M. debilis*

## COMPARISON OF SPECIES OF METADEVESCOVINA

It is not difficult to differentiate the species of *Metadevescovina* as they are diagnosed in this paper. The comparison made here is supplementary to and explanatory of the preceding key.

*Metadevescovina stereociliata* can easily be separated from all other species of the genus by its relatively broad, band-shaped trailing flagellum (pl. 35, figs. 20, 21).

*Metadevescovina polyspira* is distinct from other species in the presence of a number of rami of the parabasal body in most large specimens. In certain other species of the genus there are one or two outgrowths in occasional specimens, but in none of them is branching so frequent or so extensive as in *M. polyspira* (fig. C, 4; pl. 43, figs. 73, 74).

The closely wound spiral of the parabasal body of *Metadevescovina modesta*, with usually 3 or 4 and sometimes as many as 7 turns, characterizes that species (fig. A, 3; pl. 34, fig. 18). Some other species of the genus have several parabasal turns, but in them the spiral is typically loose.

Five species, *Metadevescovina modica, M. extranea, M. mediocris, M. debilis*, and *M. magna*, are distinct from the rest in having very short crestas, usually only about 4μ and at most 7μ. *M. extranea* (fig. A, 1) is a small species; its axostyle is slender, and its cresta is slender and inconspicuous. *M. mediocris* is also small. Its capitulum is less expanded than that of *M. extranea*, its cresta is larger, and the anterior part of its parabasal is markedly different in position (fig. A, 5). *M. modica* and *M. debilis* are larger and similar to each other in size; the former species (fig. A, 2; pl. 34, fig. 16) lacks the elaborate expansion of the capitulum which characterizes *M. debilis* (fig. C, 1; pl. 41, fig. 63). In *M. magna* (fig. C, 5), which is a good deal larger than the other species, the spiral of the capitular membrane is longer than in *M. debilis*. The anterior part of the parabasal body is inward to the capitular membrane in *M. magna* and outward to it in *M. debilis*, and in the former species the nucleus is not narrowed in the region toward the blepharoplast, as it is in the latter.

The usual shape of the cresta in devescovinid flagellates is one in which the structure narrows rapidly, beyond the anteromedial edge, and tapers gradually to its more or less pointed posterior end. In two species, *M. carina* and *M. nitida*, the cresta is broad for a large part of its length, and the anteromedial edge is often no longer than the width of a considerable part of the structure (fig. B, 5; fig. C, 2). *M. nitida* has a more elaborately developed capitulum than *M. carina*; the membrane is spiraled, forming a trough in which the anterior part of the parabasal body fits. The parabasal body is longer, and more spiraled, in *M. nitida*. The distinct gap that constantly exists between the part of the parabasal body on the anterior surface of the nucleus and the part that turns around the axostyle of *M. carina* (pl. 40, figs. 56, 57) is not present in *M. nitida* (pl. 41, fig. 60), and is one of the clearest points of distinction.

*Metadevescovina fulleri* (fig. B, 6) is similar in many respects to *M. nitida*, but the difference in the cresta is well marked and is sufficient for specific distinction. The cresta of *M. fulleri* is of the usual tapering shape; the gap in the parabasal substance is often present (fig. E, 3, 5, 6), and varies in extent. *M. fulleri* differs distinctly from *M. carina* in the cresta and in the more elaborate development of the capitulum of the axostyle. Although *M. carina* is a much smaller species, the cresta averages longer and, as noted above, is much broader in its main part than that of *M. fulleri*. *M. fulleri* always bears adherent spirochaetes (pl. 39, figs. 50, 51), and *M. carina* has none.

*Metadevescovina nudula* stands out among the remaining species in the great length of the projecting part of the axostyle, which equals or exceeds the length of the body (fig. B, 4). The nucleus is rounded in form. The other species in the same host, *M. turbula* (fig. B, 3), has, except in small individuals, a nucleus that is elongated more or less transversely and curved. An elongated and curved nucleus occurs also in *M. patula* (fig. B, 2; pl. 38, fig. 44) and *M. cristata* (fig. B, 1). The cresta of *M. patula* is longer and broader than that of *M. turbula*, and there is a difference in the shape of the longitudinal section of the parabasal, which is constricted in the former species (pl. 38, figs. 40, 44) but not in the latter. The cresta of *M. cristata* is longer than that of *M. patula*. The three species form a series in the length of cresta, and the maximum length in each is close to the minimum in the next. *M. cristata* does not have the constriction in the longitudinal section of the parabasal body. In all these species the projection of the axostyle is considerable, though much less than that in *M. nudula*.

Except in small specimens, the nucleus of *Metadevescovina cuspidata* is also somewhat elongated (pl. 36, fig. 25). It often has in general a rather quadrangular outline, with a prolongation along the trunk of the axostyle near one end, leaving a concavity in the posterior side (pl. 37, fig. 32). The prolongation and curvature are less marked than in the three species last considered. *M. cuspidata* is readily distinguished from *M. turbula* by its considerably larger cresta. In size of cresta *M. cuspidata* is closest to *M. patula*, but the trailing flagellum is stouter, and there are distinct differences in the shape of the nucleus and the parabasal body. In the parabasal body there is a clear resemblance between *M. cuspidata* and *M. cristata*, but differences exist in the anterior enlargement and the position of the posterior part. The cresta is longer in *M. cristata*, the trailing flagellum is somewhat more slender, and the nucleus is more prolonged and curved, without the quadrangular outline.

Thus it appears that, if well-developed specimens of the sixteen species are compared, it is not difficult to separate them. The variability within a species might sometimes make the status of individual specimens uncertain; but the characteristics of the nucleus, axostyle, parabasal body, cresta, and trailing flagellum, considered all together, constitute distinctive features.

## MORPHOLOGY AND DIAGNOSIS OF SPECIES OF METADEVESCOVINA

### **Metadevescovina extranea** sp. nov.

(Pl. 34, figs. 11–15; fig. A, 1)

*Type host.*—*Mastotermes darwiniensis* Froggatt. Australia.

T-516. (Cleveland.) Darwin. (Syntype slides TP-516:1, 2.)

T-309. (Cleveland.) (Xenosyntype slides TP-316:45, 48.)

*Diagnosis.*—Length 23 (13–35)$\mu$; width 12.5 (8–20)$\mu$; trailing flagellum a moderately stout cord, little if any longer than the body; cresta a slender rod, except for expansion at the anterior end, length in larger sized specimens 3.8 (2.5–4.5)$\mu$; parabasal body stout, of approximately the same thickness for its whole length, anterior part diagonal and ending at blepharoplast, from anterior end spiraled around nucleus and trunk of axostyle 1 to 3 turns; capitulum of axostyle expanded, with membranes and clear areas; trunk a slender rod, projecting a few microns from the posterior end of the body, enlargement little or none; nucleus rounded, diameter 2–4$\mu$; no adherent microorganisms.

The presence of this devescovinid in the most primitive termite greatly extends the known distribution of the subfamily, which is otherwise restricted to the Kalotermitidae.

In its anterior part the parabasal body differs from that of most species of *Metadevescovina*. There is no longitudinal section alongside the nucleus, and no extension across the anterior face of the nuclear membrane. The anterior end of the parabasal body is placed at the blepharoplast, and the spiral may be said to begin there. There is no abrupt change in direction of the parabasal, following the longitudinal section, but the slope is continuous from the anterior part, which runs diagonally alongside the nucleus. In this feature in the shape of the parabasal there is a resemblance to the much larger species *Metadevescovina debilis*. Between one and two turns of the spiral are usual, but in large specimens there may be three turns.

In the region of the nucleus, there is a structure of membranous extensions and clear areas, indicating a moderate expansion of the capitulum of the axostyle. The material was not favorable for tracing this completely, but there is some similarity to the structure in *Metadevescovina debilis* in that a trough seems to be formed into which the anterior part of the parabasal body fits. Anterior to the nucleus is a prominent clear area, which extends across the anterior end of the body. The posterior margin of this area is bounded by the membrane of the capitulum, adjacent to which is a layer of haematoxylin-staining granules.

The trunk of the axostyle is slender, and projects from the posterior end for a distance of about 5μ or less. In certain preparations the posterior part of the axostyle was stained with iron-haematoxylin, as it often is in *Devescovina*. At the posterior end of the cytosome the axostyle may be somewhat enlarged (pl. 34, fig. 12), which never happens in *Devescovina;* there is no such enlargement in most specimens of *M. extranea*.

The smoothly rounded nucleus (pl. 34, fig. 11) is made up of fine chromatin granules occupying all the interior except for a peripheral nucleolus in a clear area. The nucleus shows none of the unusual features of position, shape, or structure that characterize some more advanced species of the genus.

In several specimens there were duplicated mastigonts irregularly distributed in the common cytoplasmic mass. Eight of these were sometimes present. Such multimastigont forms, resulting from delayed division, indicate the probable mode of origin of calonymphids.

### **Metadevescovina modica** sp. nov.

(Pl. 34, figs. 16–17; fig. A, 2)

*Type host.*—*Kalotermes marginipennis* (Latreille). Mexico.

T-266. (Light 59.) Tepic, Nayarit. (Syntype slides TP-218:6, 9.)

T-263. (Light 65.) Same locality.

*Diagnosis.*—Length 52 (34–83)μ; width 25 (17–41)μ; trailing flagellum a rather slender cord, about equal in length to the body; cresta length 3–4μ; capitulum of axostyle moderately expanded, trunk without posterior enlarged cusp, projecting only slightly; parabasal body wound loosely 1–4 turns, most frequently 2–3, exceptionally as much as 7; nucleus 5–6 × 4–5μ, often somewhat irregular in outline posteriorly; surface completely covered with spirochaetes often 3–5μ long, occasionally up to 8–11μ.

The parabasal body is in its spiraled part much like that of *M. debilis*. Often the posterior part is extended straight out for a length that if spiraled would make one or two turns. In a number of specimens a part of the parabasal body was detached, lying in the posterior cytoplasm. The part remaining attached was variable in length; in one, the length equaled that of the nucleus. Detachment of the parabasal, leaving a length like this, occurs in division; but no evidences of division of *M. modica* were found in the material studied. In a few specimens the parabasal was provided with one or two rami.

In many specimens, but not in the majority, there are present on the capitulum some granules, staining deeply with iron-haematoxylin, which are larger than those on the capitulum of *M. cuspidata* (pl. 34, fig. 17). There is no posterior enlargement of the trunk of the axostyle, which projects only slightly, the end coming abruptly to a point (pl. 34, fig. 16). In all specimens there is present around the trunk of the axostyle a deep-staining filament, usually turned in a long spiral, and clearly outside the axostyle sheath. The filament could not be traced in the region of the capitulum.

The longer diameter of the nucleus is somewhat oblique in position. The substance of the nucleus is finely granular, with a peripheral nucleolus, and no clear area surrounds the chromatin mass. At one side of the nucleus, where it is met by the trunk of the axostyle, there is a pointed posterior extension, between which and the opposite side is a concavity (pl. 34, fig. 17).

### **Metadevescovina modesta** sp. nov.

(Pl. 34, fig. 18; fig. A, 3)

*Type host.*—*Glyptotermes angustus* Snyder. Panama.
T-216. Barro Colorado, Canal Zone. (Syntype slide TP-123:1.)
T-127. Same locality.

*Diagnosis.*—Length 32 (24–42)μ; width 16 (11–27)μ; trailing flagellum stout, somewhat flattened or band-formed; cresta length 10 (9.5–11.5)μ; parabasal body spiraled closely around trunk of axostyle for 1–7 turns, usually 3–4; capitulum of axostyle simple, trunk with some enlargement posteriorly, but not a prominent cusp, projection up to 10μ; nucleus 5–7μ × 4–5μ; no adherent microörganisms.

The most distinctive characteristic of *M. modesta* is its type of parabasal body (pl. 34, fig. 18). The spiral is longer than in other species of the genus. It is turned closely and smoothly around the posterior end of the nucleus and the axostyle, each turn usually being separated from the adjacent one by not more than the thickness of the structure. The diameter of the coil decreases posteriorly, the last turn often having less than half the diameter of the first. There are, however, many irregularities in the arrangement of the parabasal body in fixed material, the spiral sometimes being pulled out along the axostyle, or a turn in the spiral being a good deal wider than those adjacent to it. The parabasal filament stains deeply by appropriate methods, and is moderately stout. In its anterior, longitudinal part and in the posterior part of the spiral it is more slender than elsewhere.

The nucleus is rounded, has a small nucleolus and commonly other small deep-staining granules. In the preparations a space often existed between the membrane and the chromatin mass. The nucleus of *Devescovina arta* in the same preparations was not greatly dissimilar, but had more numerous large deep-staining granules, giving it a darker appearance. The nuclei of *Trichomonas barbouri* on the same Schaudinn iron-haematoxylin slides were stained completely black.

### **Metadevescovina stereociliata** (Grassi) comb. nov.

(Pl. 35, figs. 19–24; fig. A, 4)

*Devescovina stereociliata* Grassi, 1917, Mem. R. Accad. Lincei (5), 12:379, pl. 9, figs. 13–17.
*Devescovina stereociliata* Grassi.—Kirby, 1926, Univ. Calif. Publ. Zoöl., 29:105, fig. A, 5.—De Mello and de Brito, 1929, Arqu. Esc. Méd.-Cir. Nova Goa, (A), 5:695.—De Mello 1941, Proc. Ind. Acad. Sci., (B), 14:80, fig. 6a.

*Type host.*—*Glyptotermes parvulus* Sjöstedt. Gold Coast.
T-301. (Silvestri.) (Xenosyntype slide TP-318:1.)
*Additional host.*—*Glyptotermes* sp. nov. Uganda.
T-2072. Kampala. (Homosyntype slides TP-2017:29, 11; 2018:12.)
T-2090. Budongo Forest. (Homosyntype slide TP-2028:7.)

*Diagnosis.*—(From type host): length 43 (31–58)μ; width 21 (15–27)μ; trailing flagellum a band often about 1μ wide; cresta length 10.5 (7.5–12)μ; parabasal body coiled around axostyle 1–3, often 1½–2 times; capitulum of axostyle moderately expanded, trunk of axostyle moderately stout, tapering slightly from about 1½μ to 1μ at end of cytoplasm in large specimens, often projecting 10–15μ from posterior end, enlargement little, no angular cusp; nucleus 6–9 × 4.5–6μ, elongated in a more strictly longitudinal direction than is usual in *Metadevescovina*; group of spirochaetes adherent to the posterior end. (From *Glyptotermes* sp. nov. T-2072): length 33 (27–42)μ; width 15 (12–20)μ; trailing flagellum a band often 1μ wide, length 50–60μ; cresta length 9.5–13μ, anteromedial edge 1.5–2.5μ; parabasal body usually with about one wide turn around the posterior part of the nucleus, not more than 1½; axostyle without marked posterior enlargement, projecting often 10–15μ; nucleus 4–6 × 4–4.5μ; spirochaetes often 6–10μ long, adherent in a close-set group to the posterior part of the body.

Grassi's description and figures of this flagellate are adequate for identification, and I have examined specimens on a slide from *Glyptotermes parvulus*. One of his figures shows a rather long projection of the axostyle from the posterior end of the body—a characteristic of *Metadevescovina* which does not occur in *Devescovina*. The presence of a posterior tuft of spirochaetes is a characteristic of the species; Grassi misinterpreted these as immobile cilia and selected the species name accordingly. In a summary of the characteristics of *Devescovina stereociliata*, De Mello (1941) stated that he cannot agree with my belief that the stereocilia are attached bacteria. His opinion is not based on observations of the devescovinid, but on a supposed analogy with the situation in *Holomastigotoides*. The significance of the analogy, in proof of the question raised, is not apparent.

There are some differences between the flagellates of this species in the type host (pl. 35, fig. 19) and those in the *Glyptotermes* in Uganda. Cresta, trailing flagellum, axostyle, and adherent spirochaetes are the same. The body size of the flagellates from the former host is considerably greater, and the nucleus is larger. The parabasal body often has 1½ to 2 turns, whereas in the smaller form it is seldom as much as 1½. Grassi's figures show a length equal to the maximum I have observed, and a parabasal body with about 2 turns. It is unlikely that these differences have any taxonomic significance; even greater differences in size of body and length of parabasal spiral have been observed in *Devescovina glabra* from different colonies of *Neotermes meruensis*. There are specimens in both hosts which are alike in both size of body and size and form of parabasal structure.

The anterior part of the parabasal body is applied to the nuclear membrane, with two rather sharp bends and a relatively long limb on the anterior end of the nucleus (pl. 35, fig. 22). The posterior bend is between the middle of the nucleus and its posterior end (pl. 35, fig. 24). The posterior transverse part of the parabasal turns around the nucleus at a short distance from the nuclear membrane, or around the trunk of the axostyle, coming again close to the region of the posterior bend. In specimens from the *Glyptotermes* of Uganda the rounded end of the parabasal is usually near this point (pl. 35, fig. 22); it may stop a little short of it or extend a little beyond it. However, in specimens from the type host it often continues for another turn or two (pl. 35, fig. 19).

Along one edge of the parabasal is the parabasal filament, which is not broad (pl. 35, fig. 22). Near the anterior angle it leaves the other substance and passes directly to the blepharoplast; this arrangement was particularly clear in *M. stereociliata.* In specimens stained in Delafield after Schaudinn-fixation there is an alternation of deeply stained blocks and clear areas or vesicles in the parabasal substance (pl. 35, figs. 23, 24).

The expansion of the capitulum is moderate. The trunk of the axostyle, from an enlargement posterior to the nucleus, tapers gradually and not markedly (pl. 35, fig. 21). The projecting part of the axostyle may be a little enlarged anteriorly, but there is no sharp expansion into an angular cusp such as occurs in many specimens of *Foaina hamata,* which occurs in the same hosts. The long projection terminates in a filament.

The nucleus is smoothly rounded, except for the posterior pointed projection along the trunk of the axostyle. It is of a typical *Metadevescovina* form, with one or two deep-staining granules, fine chromatin granules or only a few larger ones, and is not deep-staining as a whole. A space around the central mass was present in the material from the type host, but not in the many better fixed preparations from *Glyptotermes* of Uganda.

I did not observe the transverse striations mentioned by Grassi. It is probable that these do not represent a normal structure. The *Fusiformis*-like rods characteristic of *Devescovina* are not present on *M. stereociliata.*

The dense posterior group of spirochaetes is usually rather sharply limited anteriorly, and no spirochaetes are present on the anterior part of the body. In the Uganda material they often covered from a quarter to a third of the body (pl. 35, fig. 20); in the type material, not so much (pl. 35, fig. 19).

The most obvious distinction between *Metadevescovina stereociliata* and its associate *Foaina hamata* is in the trailing flagellum, which is a cord in the latter species. The anterior part of the parabasal has much the same form in the two, but the anterior limb is not so long and the structure is not so stout in *F. hamata.* The posterior part of the parabasal of *F. hamata* does not spiral, but ends in a free filament passing to the periphery. There is no free filament at the end of the parabasal of *M. stereociliata.* The axostyle has a more prominent cusp in *F. hamata.* Intergrades between the two flagellates in flagella and parabasal body are absent.

### **Metadevescovina mediocris** sp. nov.

(Fig. A, 5)

*Type host.—Glyptotermes* sp. nov. Belgian Congo.
T-3018. Near Rutshuru. (Syntype slides TP-2035:2, 6; 2034:2, 16.)
*Additional host.—Glyptotermes* sp. nov. Ruanda-Urundi.
T-3022. Kakitumba. (Homosyntype slides TP-2038:9, 10.)

*Diagnosis.*—(From type host): length 23 (20–30)μ; width 12 (8–14)μ; trailing flagellum a moderately stout cord, about 1½ times the length of the body; cresta length 5–6.5μ, anteromedial edge about 1μ; parabasal body turned for a short distance across the anterior surface of the nucleus, enlarged at the anterior end not at all or very little; turned loosely around the trunk of the axostyle, always just posterior to nucleus, for about one turn, sometimes less; capitulum of axostyle simple; trunk of axostyle not stout, projecting 5–10μ in a slender cusp; nucleus rounded, 3–4μ × 2–3μ; spirochaetes, often 10–20μ long, adherent to the posterior part of the body, or to more of the surface up to the whole.

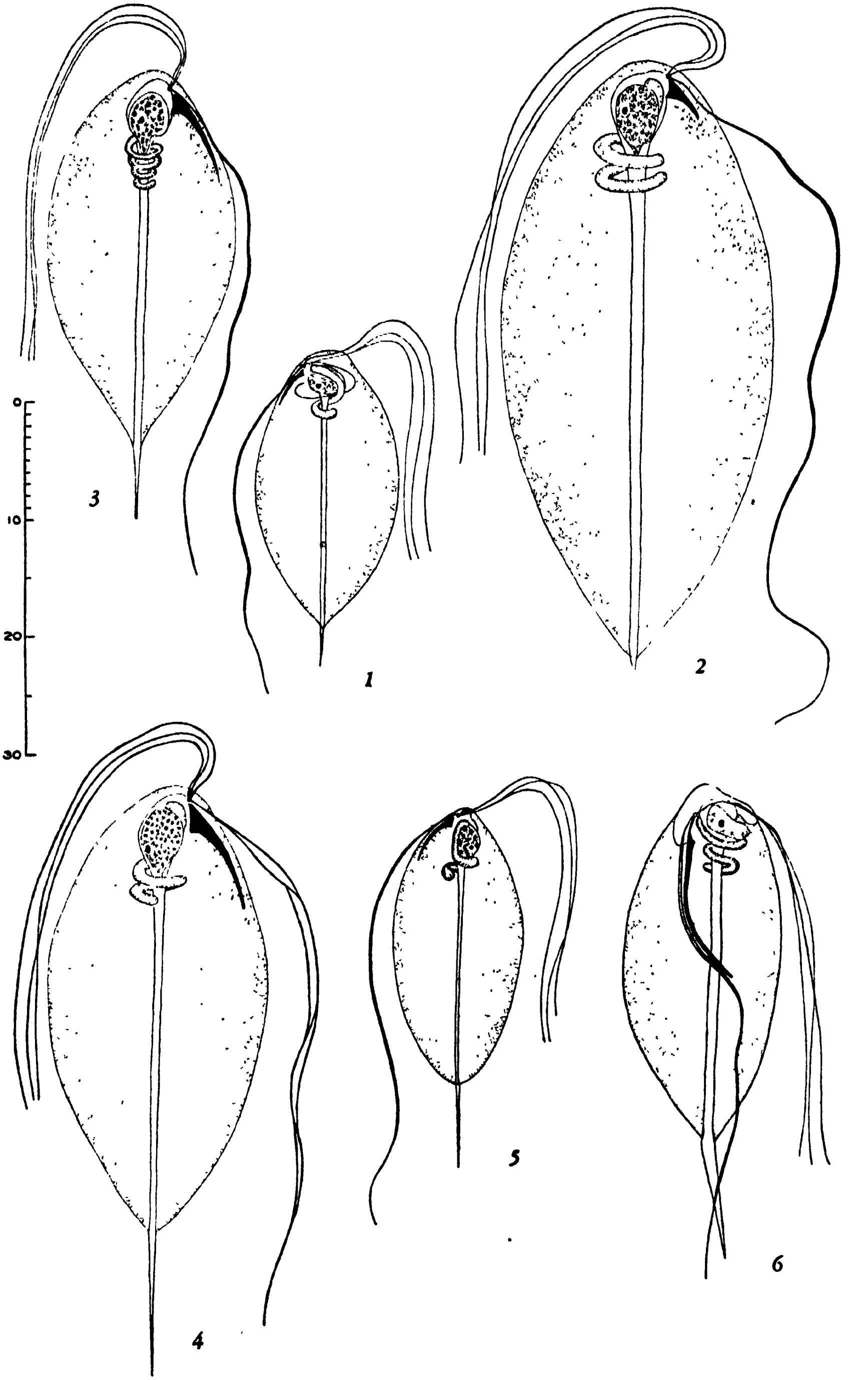

Fig. A. Species of *Metadevescovina*. 1. *M. extranea* sp. nov. from *Mastotermes darwiniensis*, Australia. 2. *M. modica* sp. nov. from *Kalotermes marginipennis*, Mexico. 3. *M. modesta* sp. nov. from *Glyptotermes angustus*, Panama. 4. *M. stereociliata* (Grassi) from *Glyptotermes* sp. nov. T-2072, Uganda. 5. *M. mediocris* sp. nov. from *Glyptotermes* sp. nov. T-3018, Belgian Congo. 6. *M. cuspidata* sp. nov. from *Kalotermes minor*. All figures and scale, × 1500.

Because of the general resemblance of the flagellate faunules of the hosts of this species to those of *Glyptotermes parvulus* and the Uganda *Glyptotermes* (T-2072), it was expected that the *Metadevescovina* would be *M. stereociliata.* There are marked differences, however, in both structural features and size. In all specimens of *M. mediocris* that were examined the trailing flagellum was a rather slender cord; in all specimens seen of *M. stereociliata* it was a rather broad band. The cresta of *M. mediocris* is narrower and in length is entirely below the range in the other species.

The species is similar in some respects to *Metadevescovina turbula,* which is somewhat larger and has a longer cresta. A notable difference from that flagellate exists in the shape of the nucleus. In *M. mediocris* the interkinetic nucleus always has a simple, rounded shape. In *M. turbula* it is characteristically elongated and curved.

*Metadevescovina mediocris* is similar in size to *M. extranea,* but there are important structural differences. In the former species the cresta is larger and more prominent than in the latter; the capitulum is simpler; the anterior part of the parabasal body is different in position and origin; and the axostyle has a longer posterior projection.

### **Metadevescovina cuspidata** sp. nov.

(Pl. 33, fig. 10; pl. 36, figs. 25–30; pl. 37, figs. 31–37; fig. A, 6)

*Devescovina* sp.—Kirby, 1926, Univ. Calif. Publ. Zoöl., 29:27.—Light, 1926, Univ. Calif. Publ. Zoöl., 29:155.—Kirby, 1931, Trans. Amer. Micr. Soc., 50: 194.

*Metadevescovina cuspidis* Kirby, 1934, *in* C. A. Kofoid, Termites and Termite Control: 92, fig. 20, *o.*—May, 1941, Trans. Amer. Micr. Soc., 60:282, 288. (Name invalid, published without a summary of characters.)

*Type host.*—*Kalotermes minor* Hagen. California.
T-8. Gilroy. (Syntype slides TP-19:9, 15.)
T-1. Mt. Diablo. Xenosyntype slides TP-18:1, 15.)
T-3. Los Gatos. Xenosyntype slides TP-16:1, 3.)
T-20. Gilroy. (Xenosyntype slides TP-229:18, 48.)

*Diagnosis.*—Length 30 (9.5–53)μ; width 12.5 (5–25)μ; trailing flagellum a stout cord, 1½–2 times the length of the body; cresta length usually 10–16μ, occasionally up to 20μ, averaging 13μ; anteromedial edge 1–1½μ; parabasal body spiraled rather closely from less than 1 turn to about 2½ turns; capitulum of axostyle moderately expanded, elevated into a ridge, and with a moderate membranous extension; trunk of axostyle stout, with prominent enlarged cusp, projection up to 10–15μ; nucleus in larger specimens 6–7μ × 3–4μ, chromatin mass often quadrangular in shape, containing moderately coarse granules; long spirochaetes usually adherent to anterior and posterior ends.

The occurrence of this flagellate in *Kalotermes minor* was mentioned by Kirby (1926) and Light (1926) under the name of *Devescovina,* and I described its parabasal body (1931*b*). In 1934, when listing the protozoa of *Kalotermes minor,* I included the name *Metadevescovina cuspidis.* Since no diagnosis was then given, the more properly formed new name is used here.

Studies of the species were made in 1929 by Miss Marie Lanfear; certain data from her unpublished report have been incorporated in the following account.

Miss Lanfear reported the following measurements: length of body (419 specimens), including the projecting axostyle, from 17.5μ to 61μ, without the axostyle, from 12μ to 53μ; width (315 specimens) from 5μ to 23μ. In my own measurements of fifty flagellates the length, not including the projecting axostyle, ranged from 17μ to 46μ, the width, from 7.6μ to 21.4μ, average 29.5 × 12.4μ. A hundred other specimens, in which special effort was made to get the largest and smallest forms, measured 9.5–50.4μ × 5.3–25μ. Because of the great variation in size, it was at first thought that two separate species might be involved. But a graph made for the length of the above-mentioned hundred specimens showed a continuous curve.

Miss Lanfear noted that whether the termites had fed on soft oak, hard oak, filter paper (for 2–3 weeks), or filter paper soaked in acid fuchsin (for 3 weeks) made little or no difference in the size of the flagellates, whereas starving for 10 or 14 days led to reduction in their size.

Mrs. May (1941) observed that in nymphs with swollen wing pads *Metadevescovina cuspidata* had a maximum length of 22μ, and most specimens were 12–13μ. In half-pigmented alates the length averaged 18μ. This reduction in size resulted from partial starvation.

The cresta is about half the length of the body, and is broadened in its anterior part, though much less than in species of *Devescovina* with crestas of similar length (pl. 36, figs. 25, 26).

The development of the capitulum is less advanced than in *Metadevescovina debilis*, but it is much more complex than the simple, flattened expansion usual in *Trichomonas* and *Devescovina.* It is only in certain large and favorably stained specimens that the structure described below has been made out, but it may be supposed that in essentials at least it is the same in all specimens.

The capitular expansion is mainly on the left side of the nucleus. The dorsal border of the axostyle meets the nucleus near the midline of the body, then turns dorsally in a sweeping curve to approach close to the blepharoplast (pl. 36, fig. 29). Beyond this the capitulum is expanded into the papilla. Close to the dorsal margin of the capitulum, the part posterior to the blepharoplast is elevated into a longitudinal or diagonal ridge within which there are numerous chromatic granules. The ventral part of the capitulum is frequently extended posteriorly into a blunt protuberance the dorsal edge of which is continuous with the ventral side of the trunk. The form of the dorsal part of the capitulum of the axostyle is somewhat variable, but for the most part it lies on the left and dorsal sides of the nucleus, and does not send a membranous expansion around this as in *M. debilis.*

There is, however, a narrow lamella-like structure which has been seen in many specimens, both large and small (pl. 37, figs. 31, 32). This stains rather deeply with iron-haematoxylin. It appears to be an extension of the ventral part of the capitulum, and it passes transversely on the left side of the capitulum just anterior and parallel to the first transverse part of the parabasal body (pl. 37, fig. 31). Thus, in position as well as form, it cannot be compared with the membranous expansion in *M. debilis,* which is continuous with the dorsal side of the capitulum and passes around the right side of the nucleus. This narrow lamella always bears a single layer of small chromatic granules (pl. 37, fig. 32).

The characteristic prominence of the spearhead-like projecting end, or cusp, of the axostyle led to the selection of the specific name. The greatest diameter in the posterior part usually coincides with the end of the cytoplasm (pl. 36, figs. 25–28). There is, as in *M. debilis,* a rather deep collar or at least a thickening of the axostylar sheath just anterior to this enlargement. Within the cusp the core of the axostyle is especially evident, being distinctly separated from the sheath by a clear space.

The parabasal body is of even thickness from its rounded anterior end near the blepharoplast to its rounded posterior end. In many larger specimens the parabasal is somewhat flattened and is about twice as broad as thick. When viewed from the edge, there appears a single row of large granules or blocks which stain well with Delafield's after Schaudinn's fluid or a saturated solution of mercuric chloride. When seen from the broad side there are two rows of granules (pl. 37, fig. 33). Sometimes the stainable substance is expanded so as to enclose the clear areas, in which case there appear two rows of vesicles (pl. 37, fig. 34). There may be a groove along the center of the broader sides of the parabasal. In small individuals the parabasal is not broadened and has a single row of granules (pl. 37, fig. 35). The apparent double structure of the parabasal body in larger individuals might be regarded as preparatory to splitting, but that is not true.

In iron-haematoxylin preparations the unstained substance of the parabasal appears homogeneous, the outlines are smooth, and there is a slender parabasal thread just within the inner edge (pl. 37, fig. 32).

Parabasal bodies with rami in the posterior part are not infrequent in this species (pl. 37, fig. 37). A considerable number of specimens have been observed in which the parabasal appeared divided, at a point variably situated, into two parts of approximately equal thickness and of equal or unequal length. One of these parts is the main parabasal, the other the single ramus. A few specimens were observed in which there were two rami, and one, out of thousands, in which there were three.

A number of specimens have been seen in which part of the parabasal was detached and situated in the posterior cytoplasm, whereas the part remaining in place had one or two coils. There were no indications of division in these specimens. It is probable that the parabasal body continues to grow during vegetative existence (suggested also by the greater number of coils in large individuals) and at times loses a substantial part of itself, which latter is resorbed. In numerous flagellates that otherwise appeared normal, the anterior limb of the parabasal, besides the nucleus, was separated into two, three, or more parts connected by slender threads.

The nucleus (pl. 36, fig. 25) is elongated in an oblique or, less frequently, a nearly transverse or longitudinal direction. In most material there is no space under the membrane. There is a pointed extension along the trunk of the axostyle, and a concavity at one side of this, much like that of *M. modica*. Besides the nucleolus, there are numerous large deep-staining granules and masses, so that the nucleus as a whole is somewhat *Devescovina*-like in its stainability. There is no marked curvature of the nucleus.

Wood particles and granules are abundant throughout the cytoplasm, and often there is an especially marked aggregation in the extreme posterior part. The region around the collar at the base of the axostylar cusp is clear or finely granular, being free of the larger inclusions (pl. 36, figs. 26–28).

The spirochaetes adherent to the surface of the body are limited almost entirely to the anterior and posterior ends (pl. 33, fig. 10). Their length is about 9–13$\mu$, and may reach 20$\mu$. Those of average size have about 2 turns in the spiral; longer ones may have 3 or 4. Mrs. May (1941) observed that there were relatively few spirochaetes adhering to the flagellates of reduced size in nymphs with swollen wing pads and in early alates. In specimens living under normal environmental conditions, however, they are generally numerous.

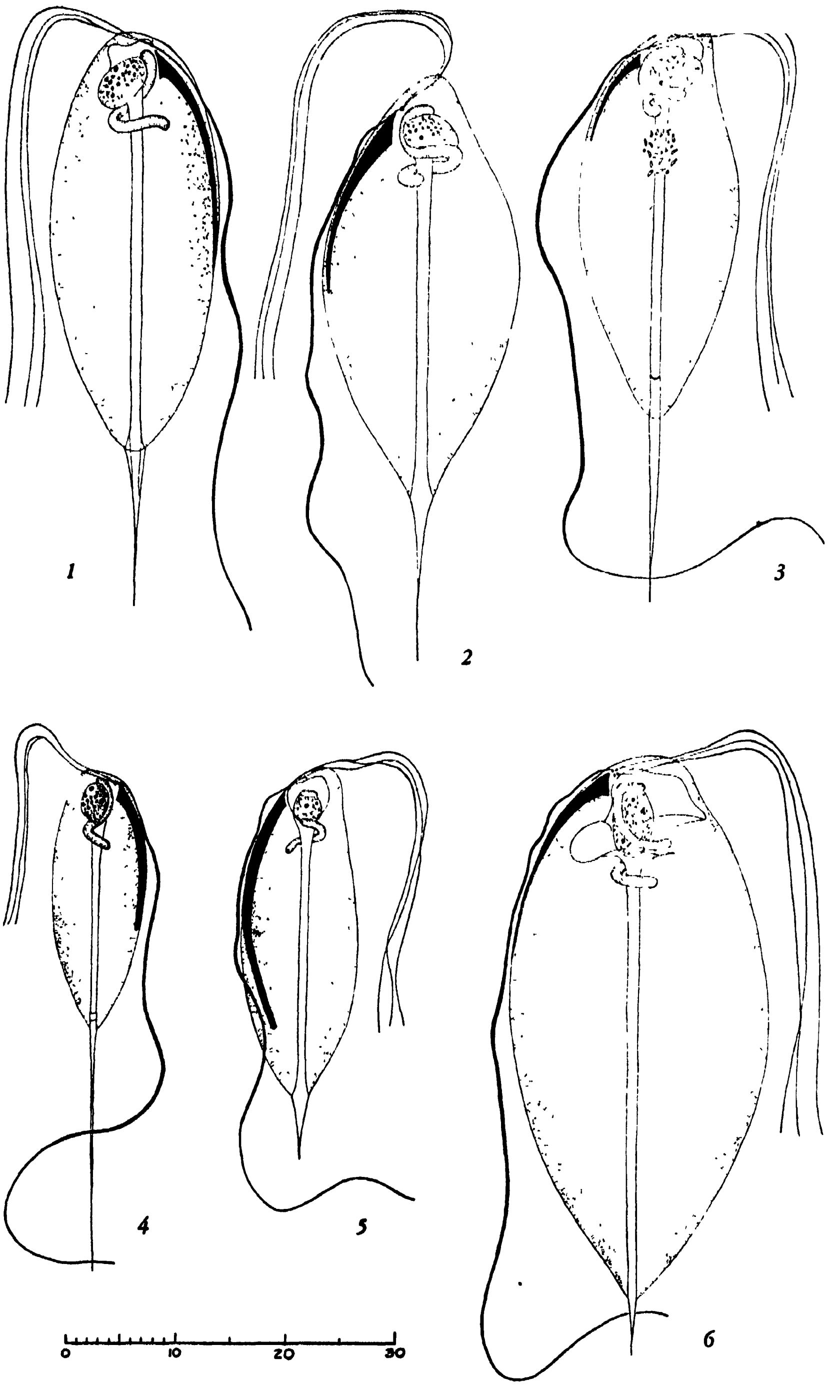

Fig. B. Species of *Metadevescovina*. 1. *M. cristata* sp. nov. from *Procryptotermes* sp. nov. T-1040, Tanganyika Territory. 2. *M. patula* sp. nov. from *Kalotermes condonensis*, Australia. 3. *M. turbula* sp. nov. from *Kalotermes jouteli*, Florida. 4. *M. nudula* sp. nov. from *Kalotermes jouteli*, Florida. 5. *M. carina* sp. nov. from *Kalotermes madagascariensis*, Madagascar. 6. *M. fulleri* sp. nov. from *Kalotermes durbanensis*, South Africa. All figures × 1500.

### **Metadevescovina cristata** sp. nov.

(Pl. 37, fig. 38; fig. B, 1)

*Type host.*—*Procryptotermes* sp. nov. Tanganyika Territory.
T-1040. Amani. (Syntype slides TP-1041:10, 14, 16.)
T-1024, 1025, 1026, 1027, 1044, 1051. Amani.

*Diagnosis.*—Length 35 (21–50)μ; width 14.5 (6–26)μ; trailing flagellum a cord more slender than that of *M. cuspidata*; cresta length 22 (17–32)μ, anteromedial edge 1½–2½μ; parabasal body turned loosely around axostyle ¾ to 1½ times, usually 1, anterior end enlarged; capitulum and trunk of axostyle similar to those structures in *M. cuspidata*, cusp longer, often projecting 12–20μ; nucleus elongated obliquely and curved, 4.5–8μ × 2.5–4.5μ, averaging 5.8 × 3.5μ; long spirochaetes, many 9–11μ, adherent to anterior and posterior ends; stout rods, many 4–5μ, often present among spirochaetes at posterior end.

The blepharoplast of *Metadevescovina cristata* is a compact group of granules to which the flagella connect directly, with no flagellar granule. The cresta is large, and is one feature that distinguishes this species immediately from *M. cuspidata*. The trailing flagellum, also, is markedly more slender than in that species.

The anterior part of the parabasal body runs longitudinally close against the nuclear membrane—not curved outward as in *M. debilis*. In most specimens there is a prominent enlargement at the end, giving the structure somewhat the form of an ax handle. This enlargement is absent in *M. cuspidata*. The winding around the axostyle is not so close as in *M. cuspidata*, the posterior part extending outward in the cytoplasm in a curve of much too large a radius to carry it around the axostyle. If this part were turned closely, as in *M. cuspidata*, the number of turns in the two species would be similar.

In preparations stained in iron-haematoxylin after Schaudinn's or Flemming's fluid a deep-staining, sharply defined parabasal thread is present along one edge of the part of the parabasal body posterior to the nucleus. It has not been observed in the anterior part.

When stained in Delafield's haematoxylin after Schaudinn's fluid, the parabasal body is shown to consist of alternating deep-staining and light-staining substance. The enlargement on the anterior end of the nucleus, and the narrow longitudinal part against the nuclear membrane, are composed entirely of deep-staining material. In the rest, the deep-staining material is somewhat less than half of the substance, forming a plate on one side. In most specimens the parabasal body is so oriented that for the full breadth of the parabasal only this plate shows. From another aspect, however, the narrower side of the plate appears, with the light-staining material beside it. The deep-staining material is continuous, not being broken up into granules or blocks. It often contains a number of small vacuoles. The light-staining material is homogeneous.

The longest diameter of the nucleus is oblique, often about halfway between longitudinal and transverse, and the trunk of the axostyle is in line with the anterior part, passing far to one side of the posterior part. There is nevertheless a pointed extension at the place where the trunk meets the nucleus.

A feature of the nucleus is its curvature. It is more or less deeply concave on the side toward the trunk of the axostyle. The curvature is similar to that of *Foaina reflexa*.

There was no space under the membrane in either Schaudinn- or Flemming-fixed

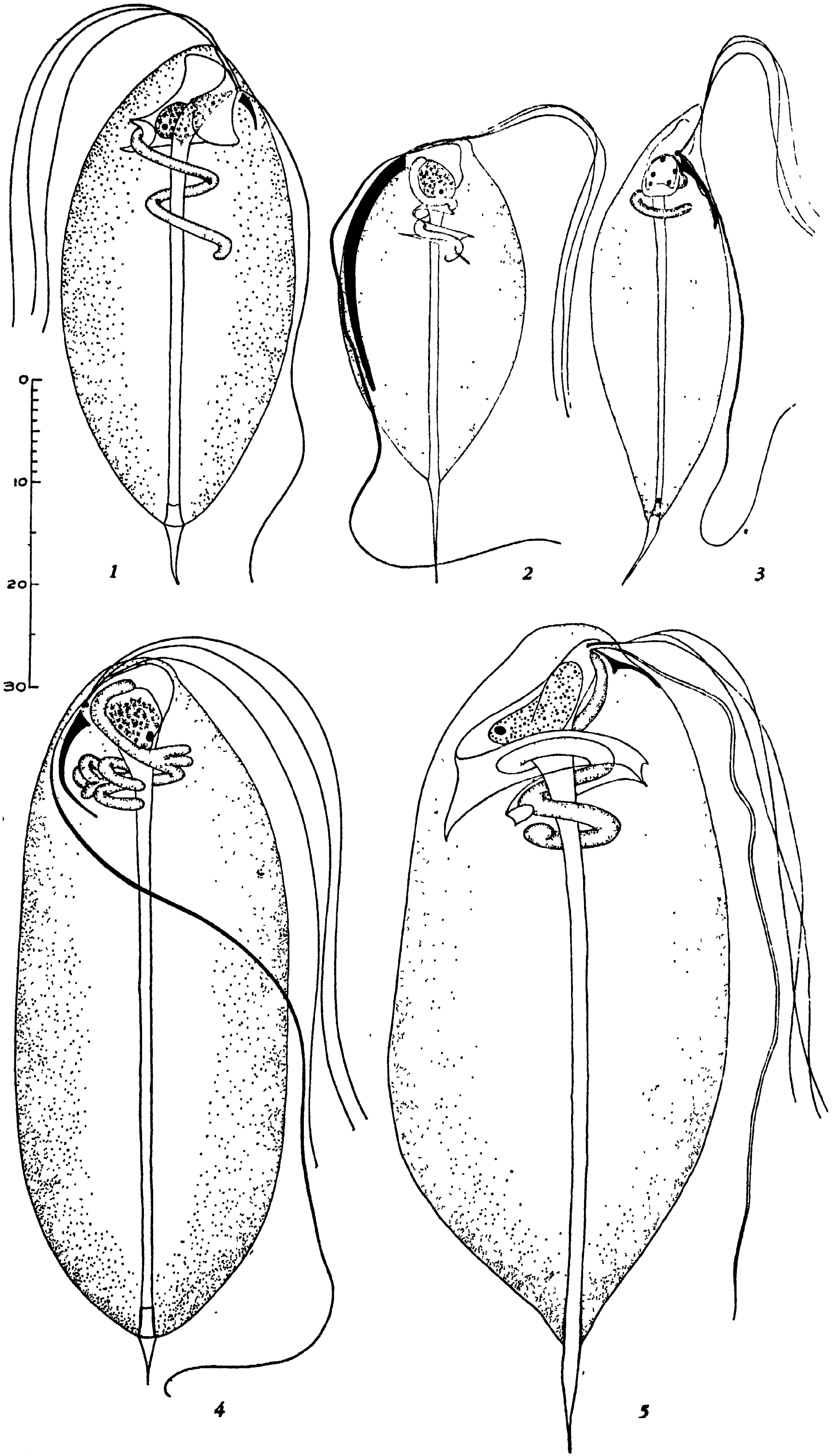

Fig. C. Species of *Metadevescovina*. 1. *M. debilis* Light from *Kalotermes hubbardi*, Arizona. 2. *M. nitida* sp. nov. from *Procryptotermes paradoxus*, Madagascar. 3, 4. *M. polyspira* (Lewis) from *Kalotermes occidentis*, Mexico. 5. *M. magna* sp. nov. from *Kalotermes marginipennis*, Mexico. All figures × 1500.

material. The chromatin granules are larger and more distinct, and stain more deeply than in some species, but they are, unlike those in *Devescovina*, uniform in size.

Intranuclear parasites, which cause enlargement of the nucleus, occasionally occur.

### **Metadevescovina patula** sp. nov.

(Pl. 38, figs. 39–45; fig. B, 2)

*Type host.*—*Kalotermes condonensis* Hill. Australia.

T-501. (Hill 3186.) Aust. Cap. Terr. (Syntype slides TP-501:10, 2, 3, 98.)

*Diagnosis.*—Length 39 (27–62)μ; width 17.5 (11–29)μ; trailing flagellum a moderately stout cord, length often 55–60μ; cresta length 14 (11–19)μ, anteromedial edge about 2.5μ; parabasal body bent across the anterior end of the nucleus, forming a cap, narrowed and flattened in one part of the longitudinal section, turned around trunk of axostyle usually only once, occasionally up to 3 times; trunk of axostyle forming a prominent enlarged cusp at the posterior end of the cytosome, projecting often 8–16μ; capitulum of axostyle moderately expanded; nucleus elongated more or less transversely and curved so as to appear grooved or concave on the left side, 6.6 (5.3–7.3)μ × 4 (3.3–4.7)μ; adherent spirochaetes usually localized at the anterior and posterior extremities.

Sutherland (1933) recorded *Devescovina striata* Foà from *Kalotermes oldfieldi* var. *chryseus* Hill. According to Hill (1942) that name is a synonym of *K. condonensis*. In the preparations from the termites collected by Cleveland and determined by Hill as *K. condonensis*, no flagellate resembling *D. striata* is present. *Metadevescovina patula* is the only devescovinid flagellate.

The blepharoplast group is an aggregate of moderate size consisting probably of four small granules. The slender roots of the anterior flagella pass directly into the group. The nucleus is located very close to the granules, so that the nuclear rhizoplast is very short. The cresta has a tapered shape, and its posterior end is rather blunt.

The parabasal body has a characteristic and unique form. The anterior part bends across the anterior end of the nucleus. The longitudinal part alongside the nucleus is flattened and narrowed so as to constitute a relatively slender connection between the parts anterior and posterior to it. This form of the parabasal body occurs as an occasional feature in many species, but it is constant in *M. patula*. Usually the parabasal is turned about once around the axostyle, not very closely; occasionally, particularly in larger animals, there are a number of close turns. In the region of the constriction, the parabasal filament separates from the other substance and extends to the blepharoplast parallel with and close to the anteromedial edge of the cresta. In one instance a bifid parabasal, with a long ramus arising at the beginning of the spiral, was observed.

The capitulum of the axostyle is developed with a moderate degree of elaborateness; but it is much less expanded than in *M. fulleri*, to which *M. patula* is similar in some respects. The trunk of the axostyle meets the posterior end of the dorsal part of the nucleus, and the flattened capitulum extends obliquely anteriad and dorsad on the left side of the nucleus. The anterior end is near the blepharoplast group of granules, which is situated on the left of the capitular membrane. From its dorsal edge the capitulum is extended in a membrane which almost completely encircles the nucleus; and is located close to it. In its proximal part this extension is broader than the nucleus and extends into the cytosome anterior to it. The membrane narrows distally. In the first part of its spiral the parabasal apparatus passes external to and against the posterior part of a section of this capitular membrane, but there is no distinct trough.

The trunk of the axostyle is stout within the cytosome and it always projects for a moderate distance. The core tapers gradually to its filamentous end. At the posterior end of the cytosome the sheath of the axostyle stands away from the core more than elsewhere, forming a prominent, spearhead-shaped cusp.

Except in smaller, probably undeveloped specimens, the nucleus is elongated transversely by development of a ventral extension. When the flagellate is oriented with the dorsal side to the observer's right, and one focuses on the main mass of the nucleus near the blepharoplast, it has a customary ellipsoidal shape. In deeper focus, moving toward the right side of the flagellate, the ventral extension comes into view. This narrows as it continues ventrad, is curved toward the left, and its end is often shifted somewhat posteriad to the transverse axis of the nucleus and is bluntly pointed. The nucleus thus is concave or grooved on the left side. The parabasal body follows closely the posterior edge of the extension of the nucleus as far as its end; it often appears as though the parabasal had separated from the ventral terminus of this extension, so closely does it follow it in its twisting.

The presence of adherent spirochaetes is characteristic of the species. These are generally localized on the anterior and posterior parts of the body; but some are often present also on part or all of the middle section.

### **Metadevescovina turbula** sp. nov.

(Pl. 39, figs. 46–48; fig. B, 3)

*Type host.*—*Kalotermes jouteli* Banks. Florida.
T-4614. Englewood. (Syntype slides TP-3294:13, 17.)
T-4616. Key Largo. (E. M. Miller.) (Xenosyntype slides TP-3296:4, 9.)

*Additional host.*—? *Kalotermes jouteli* Banks. Mexico.
T-315. (Cleveland.)
T-337. Socorro Island. (Homosyntype slide TP-290:1.)

*Diagnosis.*—Length 32 (23–39)μ; width 14 (10–18)μ; trailing flagellum a moderately stout cord; cresta narrow, length 9 (8–10)μ; parabasal body in anterior part surrounding most of the nucleus in a C-form, with no constriction, turned immediately posterior to the nucleus in about one turn; capitulum of axostyle moderately expanded: trunk of axostyle not enlarged at posterior end of cytosome, surrounded by a close-fitting sleeve 6–10μ long, projecting often 14–20μ; nucleus often elongated more or less transversely and curved so as to seem grooved or concave on the left side, size 6.1 (4.7–7.3)μ × 4.2 (3.3–5.3)μ; spirochaetes adherent to the posterior part of the body, often half or more, rather stout rods 3–4μ long intermingled with them on many specimens.

The C-shaped anterior part of the parabasal body extends around the dorsal, much of the anterior, and much of the posterior parts of the nucleus (pl. 39, fig. 48). The length of the anterior arm of the C varies; it is closely applied to the nuclear membrane and is stout throughout.

Constrictions in the longitudinal part of the parabasal occur occasionally, as in other devescovinids, but it is not the usual thing in this species, as it is in *M. patula*. The posterior part of the parabasal is turned around the trunk of the axostyle immediately behind the nucleus about one turn or somewhat less. More than one turn is unusual.

The capitulum of the axostyle has not been studied in great detail, owing to the nature of the preparations, but from what has been observed it seems to be like that of *M. patula*. The trunk of the axostyle is moderately stout in its course through the body. At the end of the cytosome it is surrounded by a close-fitting sleeve, which has a length of 10μ or somewhat less (pl. 39, fig. 46). Around the trunk anterior to the sleeve is an aggregate of a few granules, which sometimes is compact and appears in the form of two rings. Occasionally around this region there is a larger aggregate of granules. The tapering end of the axostyle projects for a variable distance.

A constant characteristic of the species is an aggregate of short rods or granules, much like that in *Devescovina glabra,* around the trunk of the axostyle anterior to the middle of the body (pl. 39, fig. 48). The anterior edge of the group is a few microns posterior to the parabasal body. The outlines of the group are diffuse and irregular; it does not have the form of a compact ring, as the similar aggregate often does in *D. glabra.* The rods or granules, which most likely are bacteria, extend a variable distance along the trunk of the axostyle, and often are arranged in the shape of a cylinder, the length along the axostyle being much greater than the diameter; sometimes they are all situated close to the trunk of the axostyle. The number of these structures varies, but very few specimens of *M. turbula* have been seen in which there were none.

The nucleus resembles that of *M. patula* in its structure, and in its transversely elongated, curved shape. In it are a variable number of spherical, deep-staining granules, which are not very closely packed. Granule-free areas in the nucleus are often apparent. A peripheral nucleolus is characteristic, but often it is unusually small in size and sometimes is not to be found. Sometimes there are two nucleoli.

Three kinds of microörganisms adhere to the body. These are intermingled on a varied extent of the surface. Spirochaetes are abundant. They are sometimes restricted to the posterior half, but in many specimens cover the whole body except the most anterior part. The name *turbula* has reference to the somewhat disorderly grouping and activity of these spirochaetes, in contrast to their absence on the associated flagellate, *M. nudula.* Adherent to the surface by one end are rods, many with a length of 3–4μ, which are much stouter than the rods that adhere full length to *Devescovina.* Their interior structure often shows a heterogeneity, stainable areas alternating with clear ones, or there are a number of chromatic granules. The rods appear to separate from the flagellates very easily, and many are found free in the smears. No differentiations in the peripheral cytoplasm of the flagellate comparable to those in *Macrotrichomonas virgosa* have been observed. Rods were abundant on the flagellates in a colony of *Kalotermes jouteli* from Englewood; but in a colony from Key Largo only a few rods were present. Numerous straight, slender, long, nonmotile filaments, which were revealed by dark-field illumination, constitute the third kind of microörganism symbiotic on *Metadevescovina turbula.*

### **Metadevescovina nudula** sp. nov.

(Pl. 39, fig. 49; fig. B, 4)

*Type host.—Kalotermes jouteli* Banks. Florida.

T-4614. Englewood. (Syntype slides TP-3294:30, 32.)

T-4616. Key Largo. (E. M. Miller.) (Xenosyntype slides TP-3296:2, 12.)

*Additional host.—? Kalotermes jouteli* Banks. Mexico.

T-315. (Cleveland.)

T-337. Socorro Island. (Homosyntype slide TP-290:1.)

*Diagnosis.*—Length 21 (11–35)μ; width 8 (4–15)μ; trailing flagellum a moderately stout cord; cresta wider than in *M. turbula,* length 12.5 (8–17)μ; parabasal body turned 1 (2/3–1.5) times in a spiral more drawn out than that in *M. turbula,* capitulum of axostyle moderately expanded; trunk

**of axostyle projecting without previous enlargement for a length equal to or exceeding that of the body, surrounded before projection by a sleeve 2μ or less in length; nucleus ellipsoidal in form, elongated more or less longitudinally; size 3.2 (2–4)μ × 2.2 (1.7–2.7)μ; no adherent microörganisms.**

There are many points of distinction between this species and the other species of *Metadevescovina* in the same host, *M. turbula*. The flagella are alike in the two, but they differ in cresta, parabasal body, nucleus, axostyle, and general cytoplasmic characteristics.

The cresta of *M. nudula* is longer and for most of its length is wider than that of *M. turbula*. When extended longitudinally it typically reaches as far as or posterior to the middle of the body; whereas in *M. turbula* the cresta always stops considerably short of the middle of the body.

The parabasal body is like that of *M. turbula* in that it curves around the dorsal part of the nucleus, with some extension on its anterior surface, and takes about one turn around the trunk of the axostyle. There is likewise no constriction in the longitudinal part. There is in general, however, a difference in the form of the spiral. In *M. turbula* the parabasal for the entire turn is close to the nucleus. In *M. nudula* it is typically drawn out, so that the posterior end of the spiral is situated somewhat more posterior to the point where it begins to turn.

The axostyle differs in the much greater length of the caudal projection, which in a number of specimens ranged from 25 to 33μ; and in the much shorter band that appears around the trunk of the axostyle just prior to projection. This band is only exceptionally visible in Hollande-fixed material, but the corresponding structures of the two species have been compared on the same slide.

The nucleus is relatively a good deal smaller than that of *M. turbula*; and it does not have the transverse elongation and curvature which characterize the nucleus of that species.

There is no aggregate of rods or granules around the trunk of the axostyle, as there is in *M. turbula*. On certain Champy-fixed iron-haematoxylin-stained slides there is a rather striking difference in the general appearance of the two species of *Metadevescovina*. The cytoplasm of *M. turbula* has a markedly yellowish cast, whereas that of *M. nudula* is gray. The difference is due not only to the included wood particles, which are yellowish or brownish in both species, but to the character of the cytoplasm. It is possible on these slides readily to separate most specimens of the two species by general appearance alone.

### **Metadevescovina carina** sp. nov.

(Pl. 40, figs. 54–59; fig. B, 5; fig. D)

*Type host.—Kalotermes madagascariensis* Wasmann. Madagascar.
T-4371. Ankilizato. (Syntype slides TP-3120:7, 3; 3148:2.)
T-4326. Majunga. (Xenosyntype slide TP-3101:3.)
T-4331. Majunga. (Xenosyntype slides TP-3115:4F, 11B.)
T-4363. Near Malaimbandy. (Xenosyntype slide TP-3121:3.)
T-4380. Near Mahabo. (Xenosyntype slide TP-3135:3.)
T-4391. Near Manja. (Xenosyntype slide TP-3144:3.)
T-4392. Near Besangoa. (Xenosyntype slide TP-3142:4.)
T-4393. Near Besangoa. (Xenosyntype slide TP-3145:7.)
T-4402. Near Tulear. (Xenosyntype slide TP-3150:1.)
T-4416. Near Tulear. (Xenosyntype slide TP-3154:11.)

*Diagnosis.*—Length 27 (15–36)μ; width 10.5 (4.5–17)μ; trailing flagellum slender; length in small specimens about twice that of body; cresta length 20 (10–26)μ, anteromedial edge 1–1½μ or less, broader than this for most of its length; parabasal turned widely and loosely around axostyle ½–1 turn, or less in small specimens, constant gap in Delafield-staining substance between the bar on the anterior end of the nucleus and the beginning of the spiral at the posterior end of the nucleus; capitulum of axostyle moderately expanded; trunk of axostyle projecting often 4–7μ in a more or less enlarged cusp; nucleus 1.5–3.5μ × 1.5–2.5μ; no adherent microörganisms.

This is a comparatively small species of *Metadevescovina.* The size range between well-developed, stout specimens measuring as much as 36 × 13μ and small slender specimens of only 15 × 5μ is considerable.

The blepharoplast is a compact group of granules. There is no separate enlargement at the end of one of the flagellar roots, like that in *M. fulleri.*

The species is remarkable for its large cresta. The cresta is not only unusually long, often when straightened out reaching to the posterior end of the body, but it has an unusual form (pl. 40, figs. 54, 57). It begins anteriorly like the usual devescovinid cresta, with an anteromedial edge about 1–1½μ, or less in small flagellates. Beyond the anteromedial edge there is a slight decrease in breadth, with a concavity on the inward side. However, instead of continuing to decrease in breadth, as is usual in devescovinids, the cresta soon broadens. For the greater part of its length its breadth exceeds the length of the anteromedial edge, though it does not surpass 2μ. From the surface of the body the cresta appears as a narrow, deep-staining band; the broadening described above is vertical to the surface of the body. In cross section it appears that the cresta is much flattened, but it is not so flat as a ribbon or the trailing flagellum of *D. lemniscata.*

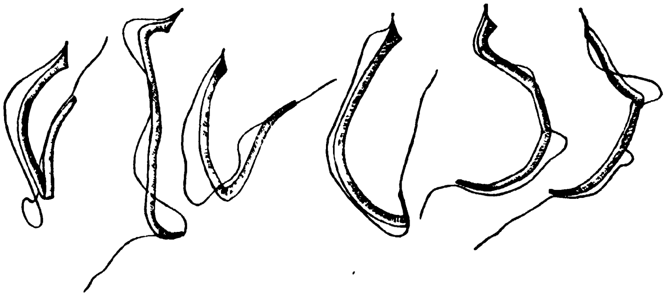

Fig. D. *Metadevescovina carina* sp. nov. Cresta and position of trailing flagellum in different fixed specimens. × 1750.

As observed both in whole mounts and in sections, the cresta stains with iron-haematoxylin more deeply in its inner than in its outer part. There is no even gradation, however. The peripheral part, often about a third or half, is, when sufficiently destained, comparatively clear, whereas the remainder is dark. This peripheral part sometimes appears undulated more than the remainder of the cresta. The course of the cresta in the body is highly sinuous and irregular, as if it were fixed during undulatory movements of considerable amplitude. The peripheral border, which stains as a definite membrane, is always at the surface of the body.

Whatever the form of the cresta, the trailing flagellum almost always follows the same course (fig. D). This is the more remarkable because for the most part in preparations there is clearly no contact between the flagellum, beyond its origin, and either the cresta or the surface of the body. The separation is often rather wide in the preparations. No observations were made on the position of the trailing flagellum in living material, but it is probable that in living material it was closer to or in contact with the surface. Separation, resulting from the technique of preparation, occurs with noteworthy ease and uniformity.

The parabasal body is unusual in form. A bar of moderate length, less than the diameter of the nucleus, appears constantly on the anterior surface of the nucleus (pl. 40, fig. 56). In all of the material examined, which came from three different colonies of termites from different areas of Madagascar, there was a gap in the parabasal body between this bar and the beginning of the spiral at the posterior end of the nucleus (pl. 40, figs. 56–59). The posterior part of the parabasal body thus begins in a position comparable to that of *Caduceia theobromae.* The parabasal filament continues as usual from the beginning of this part to the blepharoplast, passing very close to the anteromedial edge of the cresta (pl. 40, figs. 56, 57). In following this course the filament does not come into contact with the anterior bar of the parabasal, which therefore appears isolated. Observations have been made which could be interpreted as showing a direct connection of this bar, by a filament, to the blepharoplast; but the apparent connection is actually the nuclear rhizoplast. Thus, the interpretation of two separate parabasals might be made from consideration of this species alone, but this interpretation is excluded by what we know of the comparative morphology of Devescovininae.

The capitulum of the axostyle is extended into a trough in the outward concavity of which the first part of the parabasal spiral runs. No structure so elaborate as the capitulum of *Metadevescovina fulleri* and *M. nitida* has been seen. This, however, is not proof of its absence, since particularly favorable technique is required to demonstrate this, and *M. carina* is small. Only a similar part of the capitular expansion was seen in certain small specimens of *M. fulleri* in termites from Transvaal and Swaziland.

Usually the cusp of the axostyle is only moderately enlarged, but in some small specimens it is relatively enormous (pl. 40, fig. 55). The length of the projection is greater, also, in small flagellates. In Hollande-fixed material a haematoxylin-staining band around the base of the cusp was clearly demonstrated. The length of the projection is usually much less than in *M. stereociliata* (pl. 40, fig. 54).

The nucleus is rounded and small in size, with nucleolus and finely granular chromatin that destains readily. A space appeared between the membrane and the more concentrated central mass in certain Schaudinn-fixed material, but not in Flemming-fixed material in the same series nor in other Schaudinn preparations.

## **Metadevescovina fulleri** sp. nov.

(Pl. 39, figs. 50–52; pl. 40, fig. 53; fig. B, 6; fig. E)

*Type host.—Kalotermes durbanensis* Haviland. South Africa.
T-4013. Durban, Natal. (Syntype slides TP-2073:21; 2080:10.)
T-4044. Oribi Flats, Natal. (Xenosyntype slides TP-2087:1, 3, 10.)
T-4080. Riebeek East, Cape Province. (Xenosyntype slides TP-2099:11, 14.)
T-4130. Wilderness, Cape Province.

*Additional hosts.—*
*Kalotermes* sp. nov. South Africa.
T-4239. Near Warmbaths, Transvaal. (Homosyntype slide TP-3068:1.)
T-4268. Near Bremersdorp, Swaziland. (Homosyntype slide TP-3081:5.)
T-4283. Mkuzi, Zululand. (Homosyntype slides TP-3087:10, 2.)

*Kalotermes* sp. nov. Madagascar.
T-4420. Near Tulear. (Homosyntype slide TP-3153:2.)
*Kalotermes* sp. Madagascar. (*K. madagascariensis* Wasmann, acc. to Emerson *in litt.*)
T-4305. Near Maevetanana. (Homosyntype slides TP-3097:1, 16.)
T-4308. Ampijoroa. (Homosyntype slide TP-3102:3.)
T-4318. Majunga. (Homosyntype slide TP-3099:19.)
T-4336. Marohogo. (Homosyntype slide TP-3105:2.)
T-4340. 73 km. N. of Maevetanana. (Homosyntype slide TP-3104:6.)
T-4377. Near Mahabo. (Homosyntype slide TP-3108:5.)
T-4477. Near Ihosy. (Homosyntype slide TP-3174:7.)

*Diagnosis.*—(From *K. durbanensis* T-4013, 4044): length 44 (26–60)μ; width 23 (15–34)μ; anterior flagella 30–55μ; trailing flagellum a moderately slender cord, longer than body; cresta 16 (13–19)μ, anteromedial edge 1.5–2μ; parabasal spiraled loosely around axostyle one or two turns; capitulum of axostyle expanded into a broad membrane, concave outwardly, like that of *M. debilis*, trunk of axostyle tapering gradually to the posterior end, which projects 0.0–6μ; cusp of axostyle in type material usually not enlarged, but exceptions sometimes occur; nucleus 3.5–5μ × 5–6μ; spirochaetes, often 7–10μ long, adherent over most of the surface of the body, sparse on a more or less broad band anterior to or at the middle. (From *K. durbanensis* T-4130, 4080): length 38 (25–57)μ; width 16 (9–31)μ; cresta length 18 (15–21)μ; parabasal body turned loosely 1 to 2¼ times, moderately long bar present on anterior surface of nuclear membrane, forming with the other part a sharp angle close to the blepharoplast, one or two rami of parabasal rarely present; trunk of axostyle often expanded into a prominent cusp, projecting 2.5–8μ; nucleus 5 (4.5–6)μ × 4 (3.5–4.5)μ; adherent spirochaetes frequently restricted to the anterior and posterior parts of the body. (From *Kalotermes* sp. nov. T-4239): length 28 (20–36)μ; width 15 (9–22)μ; trailing flagellum a moderately slender cord, length 35–55μ; cresta length 10–14μ, anteromedial edge little more than a micron; nucleus 3–4.5μ × 2–3.5μ. (From *Kalotermes* sp. nov. T-4268): length 15–33μ; width 6–20μ; cresta 9–13μ.

In the termites from Swaziland and Zululand the body size of the limited material examined was considerably less than that of *M. fulleri* in *K. durbanensis* from Natal and Cape Province.

The blepharoplast group consists of four granules placed in an approximately square figure, with no evident enclosing matrix. The anterior flagella pass along the papilla as two roots, the posterior one stouter and deeper-staining than the other. The slender anterior root passes directly, with no enlargement, to the blepharoplast. The posterior root terminates near the blepharoplast in a well-defined, deep-staining enlargement, which generally is almost, and sometimes is quite as large as the blepharoplast group (fig. E, 1). A fine fibril connects the flagellar granule to the blepharoplast. Extending from the blepharoplast to a nearby point on the nuclear membrane is a short rod, the rhizoplast.

In Schaudinn-iron-haematoxylin material the parabasal filament along one edge is sharply defined (fig. E, 1). It is a stout filament to within two or three microns distance of its attachment to the blepharoplast. It can be traced clearly, however, all the way to the blepharoplast. In Fleming-Regaud material the parabasal filament is usually less well defined. In lightly stained specimens the deep-staining border along the anterior edge has the same size as the parabasal filament of Schaudinn-material, but in other, more deeply stained material the black part is broader and appears more as a chromophile region. In still more heavily stained material the parabasal is all black.

My material of this species shows clearly that the interpretation that the parabasal body contains a parabasal filament is correct, whereas Duboscq and Grassé's concept of the structure as in part chromophile and in part chromophobe is the result

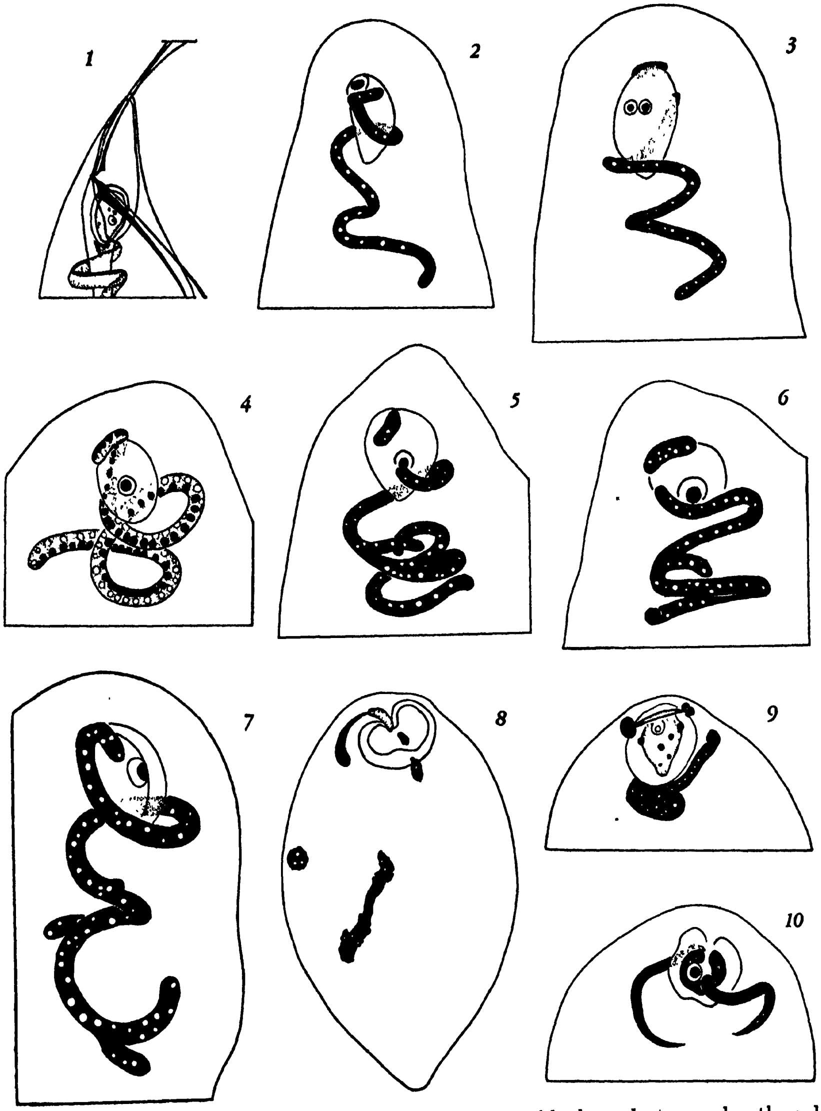

Fig. E. *Metadevescovina fulleri* sp. nov. 1. Showing the four blepharoplast granules, the enlarged root which divides into two anterior flagella, the slender root of the third flagellum to the left of this (an edge of the capitulum is shown left of this root), and the parabasal filament passing to the blepharoplast granule. The edges of the complex capitular membranes appear in the specimen, but are omitted to avoid confusion. 2. Parabasal body, structure continuous, irregular vacuolization in stainable substance. 3. Separation of the main substance of the anterior part of the parabasal body. 4. Specimen on the same slide as figs. 2 and 3, showing a row of deep-stained granules, and more light-stained substance containing clear vesicles. 5. Separation of parabasal substance anteriorly, and two rami of the parabasal body. 6. Similar parabasal with one ramus. 7. Parabasal substance continuous, with two short rami and the beginning of a third. 8. Division. Detached parts of old parabasal disintegrating in cytoplasm. 9. Division. Most of old parabasal body detached, swollen. A short piece remains at right end of the paradesmose; at the other end is a larger, curved, newly developing parabasal. 10. Later prophase, with two long, pointed, growing parabasals. The paradesmose is sunk into a deep depression in the nucleus. Fig. 1, S.H.; others, S.D. Figs. 1, 2, 4 × 1750; others, × 1800.

of moderate overstaining. The part next to the parabasal thread stains first. In sufficiently destained material the filament can be seen without difficulty.

Irregular vacuolization of the parabasal substance frequently appears, whereas another parabasal, or even another part of the same one, may show a row of granules in a clear matrix. In Schaudinn-Delafield material the parabasal body as seen from one side sometimes shows about half stainable and half nonstainable material, the stainable part consisting of a row of granules or enclosing a series of vacuoles (fig. E, 4).

The anterior bar bends across the anterior surface of the nucleus in a sharp angle from the longitudinal part (fig. E, 2). In most specimens, but not all, there is a gap of variable size between this anterior bar and the other part (fig. E, 3, 5, 6). There are all degrees of development of this gap, from a constriction of the point of separation to a space as long as the nucleus. The parabasal membrane seems to continue across the gap; it is the other substance that is lacking.

The anterior bar is not present in division stages, unless it becomes the growing part of the old parabasal, which is unlikely. The greater part of the old parabasal is detached, as in other devescovinids (fig. E, 9). The persisting part connects by its end to the blepharoplast.

The occurrence of rami of the parabasal is infrequent, and scores of individuals of all sizes may be examined without observing any. A small proportion of large individuals do have such branches. Most often, when these are present, there are one or two short outgrowths in the posterior half of the parabasal (fig. E, 5–7). Occasionally there is one long one, which may be attached to the anterior part of the parabasal body, so that for most of its length this structure appears double.

The capitulum of the axostyle (pl. 39, fig. 52; pl. 40, fig. 53) is similar to that of *Metadevescovina debilis*. The basal part lies on one side of the nucleus. This extends into a membrane that first broadens, then narrows as it turns around the body near the periphery at the level of the nucleus. It is concave outwardly in all of its course except the beginning, and is bordered by clear zones, as in *M. debilis*. The anterior part of the parabasal runs in the concavity on the outside of the capitulum, so that it follows a more or less obliquely transverse course, usually in a wide loop, unlike the situation in most devescovinids.

The trunk of the axostyle tapers from 1½μ behind the nucleus in large specimens, and projects from the posterior end for a variable distance, but generally not more than a few microns. In some specimens on smears, however, owing possibly to abnormal treatment, the trunk of the axostyle is entirely enclosed in the cytosome. There is a stainable core, which tapers gradually throughout, and a sheath. At the point of projection from the body the sheath may be separated, giving an angular enlargement of the axostyle, or it may continue to follow the core closely. In some termites most specimens lacked the enlargement, whereas in others most of them had it. Study of other devescovinids has shown that this characteristic often is variable; and some specimens were found in each host with cusps like that of the majority of specimens in the other host. In the material from the termites from Swaziland and Zululand an enlarged cusp generally occurred.

The nucleus is rounded, and often somewhat irregular in form, but with no extensions or concavities. The trunk of the axostyle meets its narrower posterior end, and the longer diameter usually extends obliquely. In the preparations some nuclei have no space under the membrane, but many have a well-marked space. Besides the nucleolus, there are a number of coarse, deeply stainable granules.

The cytoplasm contains numerous fragments of wood and often iron-haematoxylin staining spherules. One specimen was observed to contain an apparently unaltered nucleus of *Staurojoenina.*

On all the material examined, spirochaetes were present in abundance on all or part of the body (pl. 39, figs. 50, 51). On the flagellates from some colonies of *K. durbanensis* the spirochaetes were usually distributed over the entire body surface except for a band anterior to the middle; and sometimes not even that was excepted. On many of the flagellates from other colonies the spirochaetes were restricted to the anterior and posterior parts of the body. The flagellates from the Madagascar termites agreed with those from the South African hosts in distribution and abundance of adherent spirochaetes, as well as in other respects.

In suitably stained material the ends of the spirochaetes that touch the body, or are actually imbedded in the cytoplasm, as in *Pseudodevescovina uniflagellata,* appear as deep-staining granules broader than the more distal parts.

*Sphaerita* is a common cytoplasmic parasite. On the slide listed above from *Kalotermes* T-4239 almost every individual *Metadevescovina* contained from one to several sporangia. The largest sporangia were 14$\mu$ in diameter and there was room for no more than two or three of this size. Small ones were often more numerous. In this S.H. material some of the ellipsoidal spores were stained homogeneous black, but most of them were pale, with a black rod or crescent on one side.

### **Metadevescovina debilis** Light

(Pl. 32, figs. 1, 7, 8; pl. 41, figs. 61–65; pl. 42, figs. 66–70; fig. C, 1)

*Metadevescovina debilis* Light, 1926, Univ. Calif. Publ. Zoöl., 29:142, pl. 10, figs. 1–12, figs. A, B, C.—Kirby, 1931, Trans. Amer. Micr. Soc., 50:191, pl. 22, figs. 9–12.—Kirby, 1934, *in* C. A. Kofoid, Termites and Termite Control, fig. 20, *p*.—Duboscq and Grassé, 1933, Arch. Zool. exp. gén., 73:395.—De Mello, 1941, Proc. Ind. Acad. Sci. (B), 14:83, fig. 10.

*Type host.*—*Kalotermes hubbardi* Banks.
T-302. Arizona. (Light.) (Syntype slides TP-319:1, 2.)
T-252. Southern California. (Xenosyntype slides TP-189:12, 17; 191:4, 5, 6.)

*Diagnosis.*—(After Light): length 45 (30–70)$\mu$; width 20 (15–30)$\mu$; trailing flagellum longer than the body; chromatic basal rod (= cresta) short, curved; trunk of axostyle relatively large, more or less abruptly pointed or rounded at end, expanded anteriorly in a broad, flattened structure associated with internal membranes; parabasal body coiled in 3–5, sometimes as many as 7, wide turns, connected at end to blepharoplast by parabasal thread; nucleus elongated in a direction more or less transverse to the longitudinal axis of the body, extended toward blepharoplast in a long, slender, curved neck; body covered with spiral microörganisms. (Original): length 45 (31–74)$\mu$; width 22 (18–39)$\mu$; three anterior flagella about as long as the body; trailing flagellum a rather slender cord, length averaging 50$\mu$; cresta length 3.8 (3–4.4)$\mu$; parabasal body loosely spiraled, beginning at its anterior end, for 1½–4 turns, exceptionally as much as 7; capitulum of axostyle greatly enlarged in a broad, membranous expansion; trunk of axostyle stout, with moderately enlarged cusp, projecting only a few microns; nucleus 7.5 (5.5–9)$\mu$ × 3.5 (3.1–4.2)$\mu$, drawn out dorsally; spirochaetes, usually 6–11$\mu$ long, abundant on the entire surface of the body.

The blepharoplast group is apparently composed of four small granules placed close together, so that in a heavily stained specimen there appears but one unevenly outlined body about ½$\mu$ in diameter.

A description that applies to the capitulum of the axostyle has been given by

Light (1926) in part under the heading of internal membranes. My observations are for the most part in agreement with his, although my interpretation differs somewhat. Light's figures, together with those in this paper, may be used to gain a conception of the membranous expansion of the capitulum.

On the left side of the nucleus the ventral edge of the axostyle extends anteriorly, curving dorsally to a position close to the blepharoplast (pl. 41, fig. 65). From the dorsal part of this extension there arises a membranous sheet which curves around the right side of the nucleus and continues on the left side to surround the nucleus almost completely (pl. 41, fig. 62). The edges in certain positions appear as deeply stained lines. The membrane is, as noted by Light, markedly concave in its distal part, forming a trough (pl. 41, fig. 61); it narrows distally toward its rounded end on the left side of the nucleus. Anteriorly, there is an extension of the axostyle into the papilla (pl. 41, fig. 63).

The posterior margin of the capitular membrane is the anterior edge of Light's "transverse lamella," which he noted to be apparently continuous with the axostyle. However, I have not observed as such the funnel-shaped "axostylar cup" which the transverse lamella is said to constitute. The distal part of the capitular membrane is Light's "membrane of the dense triangle." His "anterior membrane" probably is a portion of its anterior part. The fibril running under the bases of the anterior flagella, from which Light believed the so-called tertiary flagella to take origin, is the anterior margin of the extension of the capitulum into the papilla. The clear areas whose form and position have been described by Light consist of the clearer cytoplasm adjacent to the membranous capitular extensions.

The trunk of the axostyle is of approximately uniform diameter to the posterior end of the body. There is a smooth outer sheath and a central core. At its posterior end the axostyle is rather abruptly pointed, often with some previous enlargement, ending in a short filament (pl. 41, fig. 61). Just anterior to the projection there is an iron-haematoxylin staining collar around the axostyle. The pointed posterior end usually projects beyond the cytoplasm, but exceptionally it is entirely enclosed. Light did not describe this projecting pointed end as constant. He described a more or less prominent protrusion of the axostyle for a length as much as four-fifths that of the body; but, as he noted, this was the result of cytolysis under abnormal environmental conditions.

Around the trunk of the axostyle in many specimens there is visible a spiral filament that stains in iron-haematoxylin (pl. 41, fig. 61). It begins near the nucleus and can be followed for a variable distance posteriorly. It may be a remnant of the paradesmose of the preceding division.

The parabasal body is a long, rounded structure, usually of the same thickness for its entire length (pl. 42, fig. 67). Its anterior end is situated close to the blepharoplast, and the spiral is continuous from this end. The parabasal body lies in the trough of the capitular membrane, as far as this extends, then is turned in a wide, loose spiral, usually of about 1½ to 4 turns, around the trunk of the axostyle. The average number of turns is about 2.5; Light reported as many as 7 turns.

In a few specimens the parabasal body was branched in its posterior part (pl. 42, figs. 68, 69). The place of origin of the ramus varied from near the posterior to near the anterior end. No specimen was observed in which the parabasal body possessed more than one ramus.

In material stained in iron-haematoxylin and suitably destained, the substance of the parabasal body is largely unstained and can be seen only with great difficulty where it runs along the capitulum. The slender parabasal filament, which stains deeply, can easily be followed to the blepharoplast (pl. 41, fig. 63). This filament is at the edge of the parabasal on the side of the inner curve, not in its center as reported by Light.

When stained in Delafield's haematoxylin the parabasal shows a characteristic heterogeneous structure, which appears in all specimens not too heavily stained (pl. 42, figs. 67, 68). There are alternating stainable granules or blocks and clear areas. The stainable elements usually are larger than the intervening clear areas and occupy the entire cross section of the parabasal, thus being like cylindrical blocks. There is some variation in the relative size of the blocks and clear areas. Sometimes the clear areas are completely enclosed by the stainable substance, appearing as vesicles, but this is by no means a usual arrangement.

In flagellates prepared by Mallory's triple stain after fixation in Zenker's fluid, the parabasal body stains blue, whereas the cresta is orange or red. When the stain is not too heavy, alternate dark blue and light blue areas are visible in the parabasal substance.

After use of the Champy-Kull technique the parabasal body is red in heavily stained material. When the stain is lighter, there appears a series of red granules or blocks with intervening areas almost or entirely without stain. Even in lightly stained material, the red parabasal filament is visible. This is the only material in which it has been possible to demonstrate the granules and the filament at the same time. Delafield's haematoxylin shows only the granules, and Heidenhain's iron-haematoxylin only the thread.

In a number of specimens the parabasal body had a degenerate appearance, manifested by constrictions in various places and a massing of the Delafield-staining substance. More frequently there is a constriction, sometimes apparently an interruption of the substance of the parabasal in its anterior part where it extends alongside the nucleus. The parabasal thread then probably binds the two parts together. In a few specimens, which showed no evidence of undergoing division, a part of the parabasal occurred free in the cytosome. The attached part was in these cases fairly long, never so short as would result from separation at the above-mentioned anterior constriction.

In some instances after rupture of the flagellate and disintegration of the cytoplasm, the parabasal body has been found to remain intact, still showing its usual structure of alternating Delafield-staining substance and clear areas.

The elongated nucleus is frequently irregular in outline, is circular in cross section, and tapers toward the blepharoplast. The position of its longer axis is usually oblique; sometimes it is almost transverse and sometimes almost longitudinal. The interior is entirely occupied by finely granular chromatin. In it there are often two or three nucleoli. Though the typical form is as just described, in some material the nucleus is in shape, position, and structure similar to that of *M. cuspidata.*

The endoplasm normally contains an abundance of wood in large and small particles, and many iron-haematoxylin staining granules. By feeding the termites on filter paper the cytoplasm can be cleared so that internal structures can be studied more readily. The wood particles are colored yellow after use of Mallory's triple stain.

In the outer cytoplasm there are often present numerous large, scattered, ellipsoidal corpuscles 1μ more or less in diameter (pl. 42, fig. 70). The corpuscles are stained red after Champy-Kull and deep blue after Mallory stain, but they are not stained by iron-haematoxylin after Schaudinn's fluid. They show up clearly in material killed in osmic acid. There is much variation in their abundance, but their presence is characteristic. They are possibly chondriosomes, but if that is so their limitation to a peripheral position is unusual. That they are symbionts is unlikely, because of their failure to stain with haematoxylin.

Adherent to the entire surface of the body there are numerous spirochaetes (pl. 32, fig. 7). These are rather broad, showing by darkfield illumination two sides distinctly separated by an optically empty area (pl. 32, fig. 8). Often there are fine, filamentous microörganisms attached among the spirochaetes. When there is a caudal projection, the filamentous microörganisms are often especially conspicuous on it (pl. 32, fig. 7). Normally the spirochaetes are continually in very active sinuous movement.

Light (1926) described the appearance and behavior of the spirochaetes, and in one of his figures (his pl. 10, fig. 2) showed some of the long filamentous microörganisms at the posterior end. He described also about twelve short, rather thick, and comparatively stiff tertiary flagella which originated in a row along the anterior border of the papilla from a fibril paralleling the basal parts of the anterior flagella (which he named the secondary flagella). My interpretation of the nature of the fibril has been given above; the supposed tertiary flagella are spirochaetes.

The proximal parts of the spirochaetes often appear thickened in iron-haematoxylin material. Light has represented this thickening (his pl. 10, fig. 2) exactly as it appears, but it is true of those not only on the papilla but also on all parts of the body. It is especially evident when the spirochaetes are observed at the edge of the body in optical section. A short terminal part of the spirochaete is often applied to the surface of the body, and this part appears thicker than the free part. At the edge of the body in optical section, it was not clear whether this thickened part was imbedded in the cytoplasm as in *Pseudodevescovina uniflagellata;* but other observations indicate that that is not true in *Metadevescovina debilis.*

Observations of living *Metadevescovina debilis* by the aid of darkfield illumination showed the spirochaetes and flagella plainly, but demonstrated no short flagella on the papilla which could be distinguished from the spirochaetes by a single instead of a double contour or a different form and type of movement. Feeding the termites upon filter paper moistened in 5 per cent aqueous acid fuchsin for twelve days brought about the death of the spirochaetes, removing them from the surface of the flagellate and leaving this smooth (pl. 32, fig. 1). Examinations were then made by darkfield illumination and in fixed and stained material. In none of the many specimens studied was it possible to find any trace of the so-called tertiary flagella, though the usual devescovinid flagellar apparatus was clearly demonstrated.

Flagellates from which the spirochaetes have been removed by feeding the host on paper moistened in acid fuchsin are somewhat reduced in size. Measurements gave a range of 26–34μ × 11–20μ, averaging 31μ × 16μ, as compared with the normal average of 45μ × 22μ. The reduction in both length and breadth amounted to about one-third.

### **Metadevescovina nitida** sp. nov.

(Pl. 41, fig. 60; fig. C, 2)

*Type host.*—*Procryptotermes paradoxus* (Wasmann). Madagascar.
T-4418. Tulear. (Syntype slides TP-3152:12, 8, 9.)

*Additional host.*—*Procryptotermes* sp. nov. Madagascar.
T-4434. Near Tsihombé. (Homosyntype slide TP-3169:9.)

*Diagnosis.*—Length 33 (14–42)μ; width 17 (6–26)μ; trailing flagellum moderately slender; cresta length 24 (13–30)μ, anteromedial edge 1–1.5μ, cresta as broad as, or broader than, this for part of its length; parabasal body turned loosely around trunk of axostyle 1–2½ turns, no gap in parabasal substance; capitulum of axostyle elaborately extended in a membrane spiraled a little more than 1 turn, formed in a long, outwardly concave trough in which the parabasal body fits; trunk of axostyle projecting often 6–15μ in average-sized specimens, with little or no enlargement; nucleus 4.5 (3–6)μ × 3 (2.5–4)μ; spirochaetes adherent to the posterior extremity and in a small group near the blepharoplast.

The blepharoplast is a compact body, which in well-stained material appears as a single large granule, though probably it is compound. There is no separation of granules and no separate enlargement of a flagellar root, as in *M. fulleri.*

The trailing flagellum and cresta are like those of *M. carina,* though the cresta is larger. As in *M. carina,* the inner part of the cresta often stains more deeply than the outer part.

The parabasal body is turned more times than in *M. carina,* the minimum in average-sized specimens of *M. nitida* being the maximum for the other species. A more significant difference than that of length is the absence of the gap in the parabasal substance alongside the nucleus, the presence of which appears to be a constant characteristic of *M. carina.*

Along one side of the nucleus, from the anterior to near the posterior end, is a broad band of granules, the chromatic shield. It is constant in occurrence, and can be seen particularly well in material in which the nucleus is well destained, except for the nucleolus.

The capitulum of the axostyle resembles that of *M. debilis,* and is more elaborately developed than has been observed in *M. carina.* The connections of the trough-like extensions with the capitulum alongside the nucleus were very clear in this material, and left no doubt of the relationship. The edges of the extension appear as well-stained filaments running parallel to the turns of the parabasal body, which are rather far apart. The extension leaves the basal part of the capitulum from the side of the tip of the papilla, and is a spiral of a little more than one turn. At its origin the membrane is about 7μ wide in an average-sized specimen. It narrows rapidly, often to 4μ half a turn farther on. It is deeply concave, forming a trough, which contains the parabasal body.

The nucleus is ovoidal in form, with its long axis in line with the trunk of the axostyle. There is a relatively large spherical nucleolus, which retains a deep stain when the rest of the nucleus has almost lost visibility, and sometimes one or two other small, deep-staining granules.

There is another difference from *M. carina* in the constant presence of two groups of adherent spirochaetes, which are not present on *M. carina.*

### **Metadevescovina magna** sp. nov.

(Pl. 43, figs. 75–76; fig. C, 5)

*Type host.*—*Kalotermes marginipennis* (Latreille). Mexico.
T-266. (Light 59.) Tepic, Nayarit. (Syntype slides TP-218:6, 9.)
T-263. (Light 65.) Tepic.

*Diagnosis.*—Length 70 (46–90)μ; width 29 (18–36)μ; trailing flagellum a rather slender cord of about body length; cresta narrow, length up to 6μ; parabasal body spiraled loosely 2–2½ turns; capitulum of axostyle greatly extended in a long, narrow spiral membrane, whose position is outward to the parabasal; trunk with projecting cusp of moderate length, enlarged somewhat but not prominently; nucleus elongated transversely or obliquely and curved, 10.5 (9–12)μ × 5 (4–6)μ; surface covered with spirochaetes 9–14μ in length.

The flagella are similar to those of *Metadevescovina modica*, which occurs in the same host. The cresta is a little longer than in that species, reaching about 6μ, and is more slender in all except its anterior part. It is shaped like a longitudinal section of an elongated rose thorn, whereas in *M. modica* it is more like an elongated triangle. *M. magna* is markedly distinct from *M. modica* in nucleus, axostyle, and the type of adherent spirochaetes.

The capitulum of the axostyle is even more highly developed than that of *Metadevescovina debilis*. There is a similar, but narrower and longer membranous expansion beginning on the right side of the nucleus, extending near the periphery of the body around the ventral and left sides, then, becoming very narrow, taking still another half turn on the right of the nucleus (pl. 43, fig. 76). The membranous expansion is concave outwardly. Anterior and posterior to the membranous capitular expansion are pronounced clear areas which give to the anterior part of the body of *M. magna* a very different appearance from that of *M. modica.*

The trunk of the axostyle ends in a rather long, tapering projecting cusp, not prominently enlarged, which is markedly unlike the short, abruptly pointed end of the axostyle of *Metadevescovina modica.* A collar surrounds the axostyle just anterior to the projection. There is often a filament along the outer edge of the trunk of the axostyle, commonly turned in a spiral.

The parabasal body is coiled loosely and rather unevenly in about 2 or 2½ turns. The anterior turns follow the capitular membrane, but are on the inner instead of the outer surface as in *M. debilis.* This difference in arrangement is an unexpected one, but there is no doubt of it.

The elongation of the nucleus is pronounced. Both ends are rounded and the breadth is approximately the same throughout, no neck being present as in *M. debilis.* The outline is somewhat irregular. The nucleus often is somewhat concave on the left side, and it occupies half or more of the distance across the body. The chromatin is in small granules, which fill the space within the nuclear membrane; and there is one rather large, round, peripheral nucleolus in a clear area. Sometimes there are also one or more aggregates of deep-staining material.

The entire body is covered with spirochaetes that are markedly longer and stouter than those on *M. modica* (pl. 43, fig. 75). The spiral has about two turns, but the spirochaetes often appear straightened in fixed material. At the posterior end there is a cluster of especially stout and deep-staining spirochaetes. The two species of *Metadevescovina* in *Kalotermes marginipennis* can readily be distinguished by the type of adherent spirochaetes alone.

### **Metadevescovina polyspira** (Lewis)

(Pl. 42, figs. 71–72; pl. 43, figs. 73–74; fig. C, 3, 4)

*Devescovina polyspira* Lewis, 1933, Univ. Calif. Publ. Zoöl., 39:84, pl. 9, fig. 21, pl. 10, figs. 22–32.—De Mello, 1941, Proc. Ind. Acad. Sci. (B), 14:78, fig. 4.
*Metadevescovina polyspira* (Lewis). Kirby, 1936, Quart. Jour. Micr. Sci., 79:311.

*Type host.*—*Kalotermes occidentis* Walker. Mexico.
T-300. Lower California. (Xenosyntype slide TP-317:14.)

*Diagnosis.*—(After Lewis): length 45 (24–94)μ; width 21 (9–44)μ; trailing flagellum slender, round, 1½ times body length; cresta length 1½ to 3 times the largest dimension of the nucleus, 15μ in one specimen; parabasal body spiraled ¾–2½ turns around axostyle, distally often branched into 2–8 parts; axostyle projecting posteriorly in short, tapering end, somewhat enlarged before projection and encompassed by a siderophile muff; chromatic mass of nucleus often lengthened transversely, with rough, uneven boundaries, dimensions of nucleus averaging 4 × 5μ, usually 1, sometimes 2 karyosomes; few adherent microörganisms. (Original): length 42 (24–69)μ; width 16 (8–34)μ; trailing flagellum a moderately stout cord, 1½ times body length; cresta length 10 (6–13)μ; parabasal body in small specimens unbranched, turned ¾–2½, usually 1–1½ times around axostyle, in large specimens branched into 2–8 strands, averaging 5; axostyle with moderately expanded capitulum and short, enlarged projecting cusp; nucleus rounded, chromatic mass sometimes irregular in shape, average size 4.5 × 5.5μ; long spirochaetes often adherent in small numbers to anterior and posterior parts of body; *Fusiformis*-like rods adherent to the surface of many small specimens.

Lewis commented upon the existence in this species of two groups of flagellates different in size and shape—a slender elongated type (fig. C, 3) and an ovoid, rotund, larger type (fig. C, 4); but he found intergrading sizes and concluded that they both belonged to the same species.

As he reported, the smaller flagellates have a simple parabasal body (pl. 42, fig. 71), and the larger ones usually have a branched parabasal body (pl. 43, fig. 73). The smaller specimens with the simple structure are in the majority. The large specimens, almost without exception, have the parabasal branched into 2 to 8, but most often 4 to 6 strands. In a few specimens I found a single ramus, like that which occasionally occurs in *Metadevescovina cuspidata*. All the strands are turned together around the axostyle.

The parabasal thread along the inside margin of all parts was described and figured by Lewis. The heterogeneity in Delafield-stained material, which was described by Lewis, is usually in the form of vacuoles in a stainable matrix. There may be a single row of them in the middle, two rows, or sometimes a middle row of large vacuoles and a row of small ones on each side. The arrangement of the vacuoles is irregular. In some parabasal bodies they extend completely across the structure, so that the stainable substance is in separate blocks.

I have been unable to verify the statement of Lewis that the axostyle is fibrillar. The capitulum seems to be similar to that of *Metadevescovina cuspidata*; a structure resembling the narrow transverse lamella of that species has been seen in *M. polyspira*, though in large specimens only. The enlargement in the posterior part of the trunk of the axostyle which is surrounded by a siderophile band and followed by a short, tapering, projecting end, was described by Lewis.

In the nucleus there is generally, in the limited material studied, a clear zone between the chromatic mass and the membrane (pl. 42, fig. 71). That mass may be angular in form, as in *M. cuspidata*.

On some small-sized specimens, with the simple parabasal body, rod-shaped microörganisms similar to those on *Devescovina* were adherent (pl. 42, fig. 72). These may be occasional in occurrence, in a manner analogous to adherence of the rods to *Foaina hilli.* Lewis stated that "cuticular striations" are not present, and I have not seen them on the larger flagellates with branched parabasal body. Spirochaetes are often present, especially on the larger specimens.

Certain dividing flagellates in prophase, anaphase, and telophase have one short, unbranched parabasal body at each pole of the mitotic figure. Other specimens in the telophase have parabasal bodies with one or several rami (pl. 43, fig. 74). Lewis showed a telophase of each type; the one with branched parabasal bodies is larger than the other, as was true of those which I observed.

The possibility that the small and large types of this flagellate may not actually belong in the same species is not excluded. The difference in size, the lack of the expected sorts of intergradation in development of the parabasal bodies, the fact that each form may divide with parabasals of its own type, and the apparent difference in adherent microörganisms, all seem favorable to the recognition of two species. But the significance of these points, as they now stand, is discounted by the lack of adequate material and by consideration of the situation in other devescovinid flagellates. I consider that the grouping of the two forms under one species is correct. The larger form, with branched parabasal body, is typical of the species.

That this flagellate belongs in *Metadevescovina* rather than *Devescovina* is indicated by the characteristics of its nucleus, axostyle, and other features. Its close relationship to certain other species of the genus should be evident from the foregoing descriptions. The large forms with branched parabasals show a certain similarity to species of *Pseudodevescovina,* but the basic organization of the parabasal apparatus is different. The rami, in *M. polyspira,* grow out from a parabasal structure that is turned around the axostyle, whereas in *Pseudodevescovina* the main limb does not so spiral, being more like that in *Foaina.*

## GENUS PSEUDODEVESCOVINA SUTHERLAND

### **Pseudodevescovina** Sutherland

*Pseudodevescovina* Sutherland, 1933, Quart. Jour. Micr. Sci., 76:160 (type species, *P. uniflagellata* Sutherland).—Kirby, 1936, Quart. Jour. Micr. Sci., 79:329.—Kirby, 1938, Univ. Calif. Publ. Zoöl., 43:10.—De Mello, 1941, Proc. Ind. Acad. Sci. (B), 14:84.

*Diagnosis.*—Size moderate to large, body stout, in known species range in length from 40 to 140$\mu$; three anterior flagella; relatively slender trailing flagellum shorter than the body; cresta of small or moderate size; parabasal apparatus consisting of a proximal element extended transversely in the region of the nucleus, not turned around the axostyle, and a number of branches or rami attached to this; capitulum of axostyle moderately developed; trunk of axostyle stout for most of length, tapering to cusp, enlarged or not, that projects posteriorly beyond the cytoplasm; nucleus of the *Foaina-Metadevescovina* type; in known species an investment of spirochaetes over almost the entire body, longitudinally adherent rod-shaped microörganisms absent.

## TAXONOMY AND DISTRIBUTION

In 1936, when I first considered *Pseudodevescovina*, a similarity to *Caduceia* was discussed. This was, however, only a superficial similarity. *Caduceia's* nearest relationship is with *Devescovina;* the two genera have the same sort of sharply tapering, entirely enclosed axostyle, and a parabasal body turned around the axostyle in a loop or spiral. The closest relationship of *Pseudodevescovina* is to the larger species of *Foaina* with branched parabasal apparatus. There is, in fact,—as is true of *Devescovina* and *Caduceia*—no abrupt separation between the two genera. The proximal element of the parabasal apparatus of *P. uniflagellata* is essentially similar to that of *F. hamata;* that of *P. ramosa* is similar to the structure in *F. reflexa.* It is not possible to use the presence of rami in the parabasal apparatus as diagnostic of the genus. Certain species of *Foaina* have a branched parabasal apparatus but otherwise are in essential agreement with species that do not; and in *Devescovina, Caduceia, Macrotrichomonas,* and *Metadevescovina* generic distinction cannot be made on that basis. The species of *Foaina* with a branched parabasal apparatus are small or moderate in size and have the *Foaina* type of long trailing flagellum and cresta. In *Pseudodevescovina* the trailing flagellum is relatively short, the parabasal body is large and branched, and the flagellate is of large size.

Grassé (1938) has recognized the genus *Pseudodevescovina.* He suggested that a difference in the type of parabasal apparatus, such as he observed in the two species he described, may warrant generic distinction. I once thought so also, when the genus *Crucinympha,* now withdrawn, was established (1938). I think there is significance in the difference between spiraling and transverse extension of the main limb of the parabasal; but certainly no generic distinctions can, in general, be based on the manner in which, in other respects, rami are given off.

## MORPHOLOGY AND DIAGNOSIS OF SPECIES OF PSEUDODEVESCOVINA

### **Pseudodevescovina uniflagellata** Sutherland

(Pl. 44, fig. 77; fig. F)

*Pseudodevescovina uniflagellata* Sutherland, 1933, Quart. Jour. Micr. Sci., 76:160, text fig. 7.—Kirby, 1936, Quart. Jour. Micr. Sci., 79:311, pls. 12–16, figs. 1–31.—De Mello, 1941, Proc. Ind. Acad. Sci. (B), 14:85, fig. 12.

*Type host.*—*Neotermes insularis* White. Australia.

T-308. (Cleveland-Hill.) (Xenosyntype slides TP-320:66, 70, 198.)

*Diagnosis.*—Length 73 (52–95)μ; width 41 (26–60)μ; anterior flagella often about 30μ long; trailing flagellum little if any longer and but little stouter; cresta length 16 (11–20μ), anteromedial edge often about 2.5μ, cresta capable of sinuous movements; capitulum of axostyle expanded, with a more or less cylindrical appendage extending posteriorly from the part in the papilla; trunk of axostyle with short, slender posterior projection; parabasal apparatus comprising an L-shaped or C-shaped proximal element, to the posterior, transverse part of which are attached usually 7–19 cords 25–30μ in maximum length; trunk of axostyle about 3.5μ broad at contact with the nucleus in large specimens, tapering to about 1μ near the posterior end, then sharpened to a point that usually projects from the body; nucleus 9.8 (7.3–12.5)μ × 5.6 (4.2–7.3)μ; body covered with a dense investment of spirochaetes often 8–10μ long.

The terms which I used (1936) in orientation of this flagellate should be altered; what was then regarded as dorsal is now considered to be ventral.

The blepharoplast group is composed of several granules, which usually are not so far apart that they are isolated from one another. When the group is well stained it shows more definitely as the compact center of attachment of the anterior flagella, trailing flagellum, cresta, and other structures than was indicated in some of my 1936 figures. This is the organization typical of most Devescovininae. There is no separate enlargement of one of the flagellar roots.

The parabasal apparatus, with its L-shaped or C-shaped proximal element and the 7–19 long rami attached to the transverse part of this, was described in detail previously. The significance of certain structures has become clearer, however, in consequence of more study of devescovinid parabasals. That is particularly true of the attachment to the blepharoplast, which is not decisively described in my earlier account, although everything that was described has been verified.

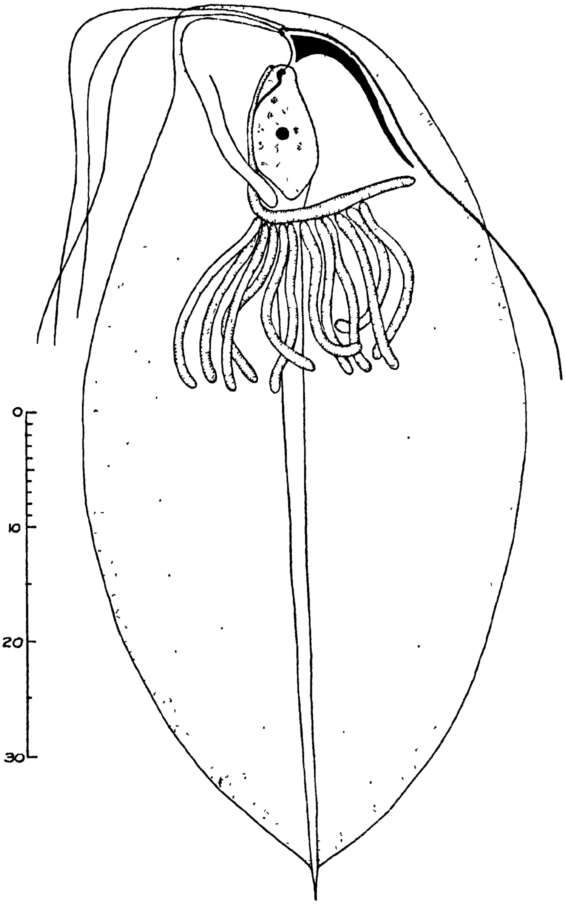

Fig. F. *Pseudodevescovina uniflagellata* Sutherland. Diagram showing the three anterior flagella and trailing flagellum; the cresta; the axostyle with its moderate capitular expansion, and the cylindrical appendage extending posteriorly from the part in the papilla; the blepharoplast group of several granules; the parabasal apparatus, consisting of an L-shaped proximal element along the lower limb of which twelve rami are separately attached, with a separated parabasal filament, enlarged against the nucleus, extending along the anteromedial edge of the nucleus to a blepharoplast granule. The spirochaetes that are attached to the surface of all specimens are omitted from this diagram. × 1500.

A stout filament, which was seen in living material, extends along the margin of the transverse part of the proximal element and separates from the longitudinal part; this is clearly the same as the parabasal filament similarly situated in many devescovinids. Its anterior part lies close against the nuclear membrane, following its contour, and there is a wedge-shaped, deep-staining enlargement near the anterior end of the nucleus. All this was clearly seen before, but the fact that the filament continues along the anteromedial edge of the cresta to the blepharoplast was not then ascertained. This is the same as in other devescovinids, except for the enlargement and the position against the nuclear membrane. It may be that this unusual development is to serve the purpose of support of the large parabasal apparatus, as was suggested before—a support more effective than is necessary when the apparatus is small or is coiled around the trunk of the axostyle.

The chromatic band which appears in well-stained iron-haematoxylin material along the transverse part of the proximal element (1936, pl. 13, fig. 2), separates on further destaining into two parts: one, a continuation of the parabasal filament along the posterior margin; the other, a band that is broader than this and mostly separate from it, anteriorly ending abruptly at the region of the bend (1936, pl. 13, fig. 5). But the earlier account was incorrect in stating that the filament is separate from the band, for after extending parallel for some distance they may meet. If the staining is heavy enough they cannot be seen separated at all. With extreme destaining the filament does not show and the band is reduced in thickness to a filament.

The filament from the blepharoplast group to the nuclear membrane, which appears in plate 13, figures 2 and 6 (1936), is the nuclear rhizoplast. In the former figure it appears to end in an enlargement, but this has not been seen frequently enough to be recognized as a constant characteristic. As in other devescovinids, this rhizoplast is close to the anterior end of the parabasal body, which here ends without bend or enlargement close to the blepharoplast group (1936, pl. 12).

The cylindrical appendage, which extends from the main part of the capitulum in the papilla to the posterior part of the nucleus on the opposite side from the main part, is an unusual characteristic. It was very clearly demonstrated.

Grassé (1938) has observed that the ends of the spirochaetes covering *Caduceia theobromae* are imbedded in the ectoplasm, stain more intensely than the rest, appear enlarged and may simulate granules. I described this (1936) in *Pseudodevescovina uniflagellata.* Grassé's suggestion that the enlargement may be in part not the spirochaete itself, but a modified host cytoplasm, is reasonable.

## **Pseudodevescovina ramosa** Kirby

(Pl. 44, fig. 78; fig. G)

*Pseudodevescovina ramosa* Kirby, 1938 (March 9), Univ. Calif. Publ. Zoöl., 43:11, pl. 2, figs. 9–13; pl. 3, figs. 14–16; pl. 6, fig. 45; fig. C.

*Type host.*—*Neotermes* sp. nov. Tanganyika Territory.

T-2012. Mt. Meru, near Usa. (Syntype slides TP-1085:13; 1082:4, 22.)

*Diagnosis.*—Length 76 (40–113)μ; width 42 (27–60)μ; anterior flagella shorter than the body, except in small individuals; trailing flagellum a relatively slender cord often about half the length of the body; cresta length 6.5 (5.3–7)μ; parabasal apparatus composed of (1) a long main limb, which is a chromophile band and filament except in its proximal part, and which extends more or less transversely after bending in a U around one end of the nucleus, (2) a short curved branch arising near the bend of the U, and (3) a voluminous branched part that arises in 1–3 trunks which lie close together near the bend of the U and subdivide at various points to produce 9–16 cords, which wind rather closely around the axostyle just posterior to the nucleus; trunk of axostyle stout, with a short, slightly enlarged, projecting cusp; capitulum of axostyle considerably expanded; nucleus with longer axis oblique in direction and curved, with one or two peripheral nucleoli, 11.8 (8.5–15)μ × 6.6 (4.4–8.8)μ; elongated granules present just under the surface of the entire body; spirochaetes, many 7–8μ long, abundant on the entire surface.

The blepharoplast group consists of a small compact granule to which the flagella, cresta, and parabasal body attach, and posterior to it a larger, deeper-staining granule or pair of granules.

The rhizoplast, which is relatively long since the distance between the blepharoplast and nucleus is considerable, has a sinuous curve and ends in contact with the nuclear membrane with no terminal granule or marked enlargement. It is represented (Kirby, 1938) in figure C, 2. In the text at that time reference was made to figure C, 1 as also showing the rhizoplast; but it does not. The filament there

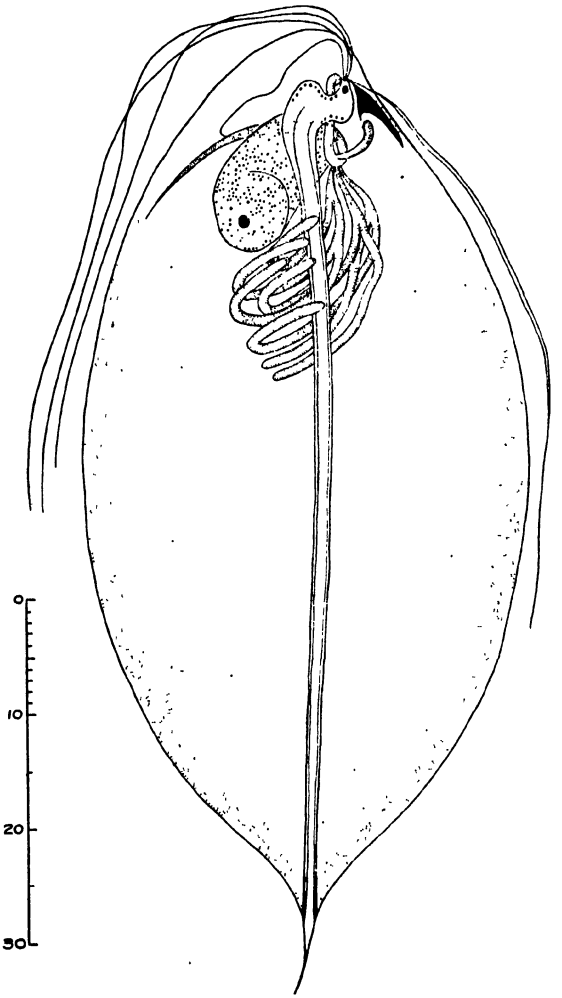

Fig. G. *Pseudodevescovina ramosa* Kirby. Diagram showing the flagella; the small cresta; the blepharoplast group of a small granule to which flagella, cresta, and the parabasal body are attached, and posterior to this a larger granule; the expanded capitulum of the axostyle, and the trunk of the axostyle that extends without enlargement to a more anterior position than is customary in devescovinid flagellates; the obliquely elongated, curved nucleus; and the complex parabasal apparatus. The proximal element of the apparatus bends in a U at one end of the nucleus, and continues transversely behind the nucleus to the edge of the body; the ramus system is attached in three trunks, which subdivide into numerous rami. The spirochaetes that cover the surface of all specimens are omitted from the diagram. × 1500.

represented, which runs along the anterior part of the parabasal body, is the parabasal filament, and its connection to the blepharoplast is clear. Free of this parabasal filament is a bent anterior hook of the parabasal, shown in figure C, 3.

There is much similarity between the complex parabasal apparatus of this flagellate and that of *Pseudodevescovina brevirostris* described by Grassé (1938). The two flagellates differ in some degree, according to the descriptions. Comments on Grassé's description of the parabasal apparatus are given below in the account of *P. brevirostris* (p. 289).

The peripheral granules of *P. ramosa* resemble in shape and position the bacteria which Grassé described as found immediately beneath the surface layer of *Pseudodevescovina punctata.* Though they seldom reach the length he gives as the maximum, 1.3μ, they seem in general to be of similar size. There is a tendency to think, as Grassé (1938) did, that the similarly situated but much smaller granules of *Pseudodevescovina uniflagellata,* which I described (1936) as imbedded ends of the spirochaetes, may also be bacteria. But in *P. ramosa* the granules do not correspond in abundance and distribution to the spirochaetes, whereas in *P. uniflagellata* they do, appearing always to be at the ends of the spirochaetes.

The spirochaetes covering the surface are notably longer than those of *Caduceia nova,* which is present in the same host.

### **Pseudodevescovina punctata** Grassé

(Fig. H, 1, 2)

*Pseudodevescovina punctata* Grassé, 1937, C. r. Soc. Biol., 125:919 (*nomen nudum*).—1938 (April 20), Bull. Soc. Zool. France, 63:117, fig. 4, A, B.

*Type host.—Neotermes aburiensis* Sjöstedt. Ivory Coast.
Pierre P. Grassé.

*Diagnosis.*—(After Grassé): length 100–140μ; width 35–53μ; trailing flagellum about half the length of the body; cresta not described; complex parabasal apparatus composed essentially of an axis which bears on one side long parabasalia often bifurcated or trifurcated; axostyle not enlarged in a capitulum; discoid nucleus; spirochaetes 10–25μ long adherent at the anterior end and in a dense tuft at the posterior end; bacteria, elliptical in form and a maximum of 1.3μ in length, distributed just under the surface layer of most parts of the body, giving it a punctate appearance.

Grassé (1938) cited the date of this species as 1937, when the name was published in a brief note on the parabasal apparatus and mitosis. It was accompanied there, however, by no indication, definition, or description, and no figure, and the host was not named; so that under the rules of zoölogical nomenclature the name as of 1937 has no status of availability or validity. In 1938 Grassé published the diagnosis and other data.

According to the measurements given, *Pseudodevescovina punctata* is an unusually long flagellate. The maximum length is approached by *P. ramosa* and by species of *Caduceia;* but the minimum of 100μ is much greater than that of any devescovinid flagellate which I have seen.

Grassé's figures, which were intended chiefly for representation of the adherent microörganisms, show only the anterior part of the body without detail; and since there is much in the structure of the animal that is still undescribed, a comparison with other devescovinids must be very incomplete.

The flagellar apparatus resembles that of *P. ramosa.*

A broad chromatic fibril is shown describing an oblique semicircle at the periphery of the body at the level of the anterior part of the nucleus, and spirochaetes adhere to the surface along this. It is said to be in relation with the blepharoplast system, and is doubtfully designated costule (cresta) in the diagnosis. I am confident that this is not a cresta, but is homologous with part of the proximal element of the parabasal apparatus of *P. ramosa,* which has the same shape and position. That being so, Grassé's description of the parabasal apparatus must be very incomplete and inaccurate; and possibly there is more similarity to that of *P. ramosa* and *P. brevirostris* than the figures indicate.

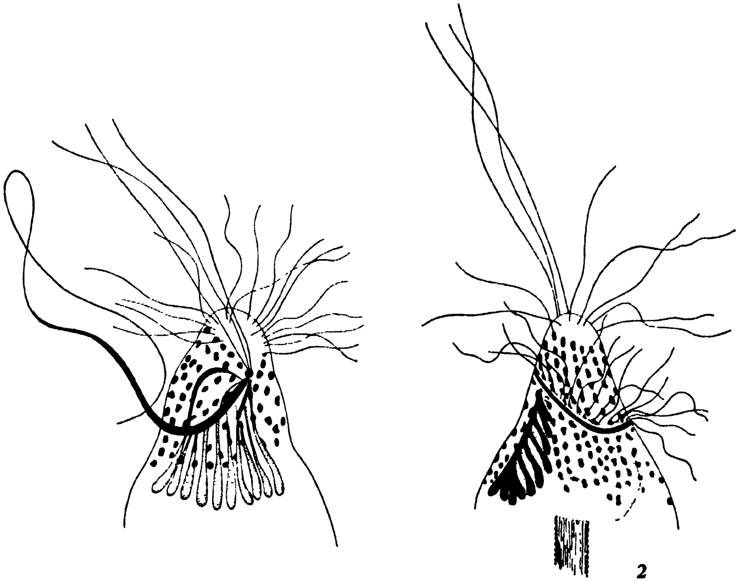

Fig. H. *Pseudodevescovina punctata* Grassé. The numerous large granules are bacteria, which are distributed just under the surface layer of most parts of the body. Long spirochaetes adhere to parts of the body. There are three anterior flagella and one trailing flagellum. The parabasal apparatus is probably incompletely represented in these figures. After Grassé, 1938. × 1000.

The spirochaetes adherent to the surface are evidently similar to those on *Metadevescovina cuspidata.* They are much longer than those that cover other species of *Pseudodevescovina.* Grassé described them as adherent principally to three regions: an area on the rostrum, along the chromatic fibril, and in a very dense tuft at the posterior extremity. He stated that elsewhere on the body there are here and there very fine spirochaetes that are difficult to demonstrate. There are no such long spirochaetes on *P. ramosa.*

The species owes its name *punctata* to the bacteria present immediately beneath the surface layer of the body. They are elliptical in form and 1.3$\mu$ long at most, and transverse division was observed. Each one is surrounded by a colorless halo, which Grassé interpreted as a capsule. The bacteria are reported to be absent from the anterior area to which the spirochaetes adhere. In the anterior part of the body Grassé noted an arrangement in sinistrally spiral rows, and considered this arrangement to be induced mechanically in consequence of the helicoid progression of the flagellate.

These granules are clearly the same as the peripheral granules of *P. ramosa,* which I also (1938, p. 14) considered microörganisms. In them there is also a surrounding clear space, such as surrounds many objects in the cytoplasm, but it would be hazardous to conclude from such a circumstance alone that one is observing encapsulated bacteria. In *P. ramosa* there is no alignment in spiral rows, although probably the motility of the flagellate is the same and the peripheral granules would be subjected to the same mechanical influence (if there is any such influence on granules in the cytoplasm, which seems unlikely).

Grassé mentioned pre- and postcystic stages of *P. punctata* and stated that in them the granules invade the entire endoplasm. My material of *P. ramosa* contained no stages that could be interpreted as in any way cystlike; the endoplasm, however, always contains an abundance of granules that resemble the peripheral granules, although they are somewhat smaller.

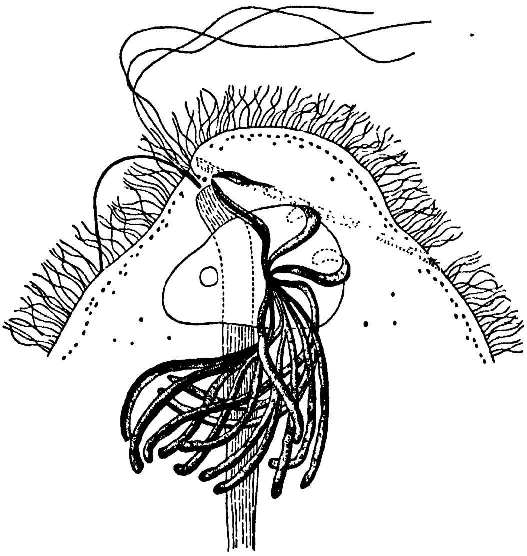

Fig. I. *Pseudodevescovina brevirostris* Grassé. After Grassé, 1938. × 1500.

### **Pseudodevescovina brevirostris** Grassé

(Fig. I)

*Pseudodevescovina brevirostris* Grassé, 1938 (April 20), Bull. Soc. Zool. France, 63:118, fig. 5.

*Type host.*—*Neotermes aburiensis* Sjöstedt. Ivory Coast.
Pierre P. Grassé.

*Diagnosis.*—(After Grassé): size a little less than that of *Pseudodevescovina punctata;* like that species in flagellar apparatus, nucleus and axostyle; parabasal apparatus with an axis to the posterior end of which are attached numerous parabasalia 8–15$\mu$ long, which are turned in a spiral around the axostyle; entirely covered with slender spirochaetes 7–10$\mu$ long; a very irregular layer of minute bacteria at a depth of 2–3$\mu$ below the surface.

*Pseudodevescovina brevirostris* resembles *P. ramosa* in all respects except that the peripheral granules, not having been reported by Grassé, seem to be absent, and the axostyle has no capitular enlargement.

The parabasal body is drawn admirably in Grassé's figure, which is reproduced here (fig. I), and only one change is necessary to make it agree with my interpretation of the apparatus in *P. ramosa.* One of the two anterior branches, which extend partly around the nuclear membrane, should perhaps be continued in the filament which forms a semicircle at the periphery of the body, and which is indicated rather indefinitely in the figure. The other rami would then be attached not at the end of the proximal element, as Grassé supposed, but at the bend of the U-shaped structure. The rami are attached in a few trunks, and branch distally. The number of rami shown corresponds to the number in many specimens of *P. ramosa.*

Grassé described the axostyle as not enlarged in a capitulum. It seems possible to me, however, that in this feature, too, *P. brevirostris* can be compared with *P. ramosa.* In *P. ramosa* the axostyle extends along the left side of the nucleus, without marked enlargement, until it reaches the vicinity of the blepharoplast. There is then a considerable membranous expansion on the dorsal and left sides. But consideration of the former part alone, which is not unlikely since it is often the most conspicuous part (Kirby, 1938, pl. 3, fig. 15), could easily mislead one into believing that there is no capitular expansion. The expansion alongside the nucleus is more marked in most devescovinids. As regards the anterior part of the axostyle, a figure similar to that which Grassé gave for *P. brevirostris* could be derived from certain specimens of *P. ramosa.*

## SUMMARY

Descriptions are given of sixteen species of *Metadevescovina* Light. Of their names thirteen are new: *M. carina, M. cristata, M. cuspidata, M. extranea, M. fulleri, M. magna, M. mediocris, M. nitida, M. modesta, M. modica, M. nudula, M. patula,* and *M. turbula.* Of the remaining names one, *M. stereociliata* (Grassi), is a new combination.

All except *M. extranea* occur in termites of the family Kalotermitidae, which as restricted by Emerson contains only the *Kalotermes*-group of genera. *M. extranea* occurs in *Mastotermes darwiniensis.* Of the nineteen termites that contain *Metadevescovina,* only two harbor more than one species of that genus; each of those has two species. Twelve species of *Metadevescovina* have only one host each; host specificity is marked in the genus.

In *Metadevescovina* the parabasal body is turned in a spiral around the axostyle. The genus differs from *Devescovina* in that the trunk of the axostyle is relatively stout to the end of the cytosome, and projects posteriorly; the nucleus is less rich in blocks of chromatin material, does not so regularly have a clear space between the chromatin mass and the membrane, is often elongated or irregular in outline; and usually lies with its longer diameter oblique or transverse. In some species the capitulum of the axostyle is elaborately developed in membranous extensions. Rodlike microörganisms are not regularly adherent full length to the surface, as in *Devescovina.*

Accounts are given of four species of *Pseudodevescovina,* all of which have previously been described. One of them occurs in a species of *Neotermes* in Australia, the others in two species of *Neotermes* in Africa. These flagellates are notable for their large size and the extensive branching of the parabasal apparatus. The trailing flagellum is relatively short. The capitulum is moderately expanded; that of *P. uniflagellata* bears a cylindrical, posteriorly directed appendage.

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# PLATES

All figures have been drawn with the aid of the camera lucida.

Abbreviations for methods of preparation: C., Champy's fluid; D., Delafield's haematoxylin; F., acid fuchsin; Fl., Flemming's fluid; H., Heidenhain's iron-haematoxylin; R., Regaud's haematoxylin; S., Schaudinn's fluid.

## PLATE 32

Drawings made from darkfield observations of living flagellates.

Fig. 1. *Metadevescovina debilis* Light from *Kalotermes hubbardi.* Specimen from termite fed for several days on filter paper moistened with 5 per cent aqueous acid fuchsin. Spirochaetes absent. × 847.

Fig. 2. *Foaina delicata* Kirby from *Glyptotermes iridipennis.* Specimen of maximum size. × 1235.

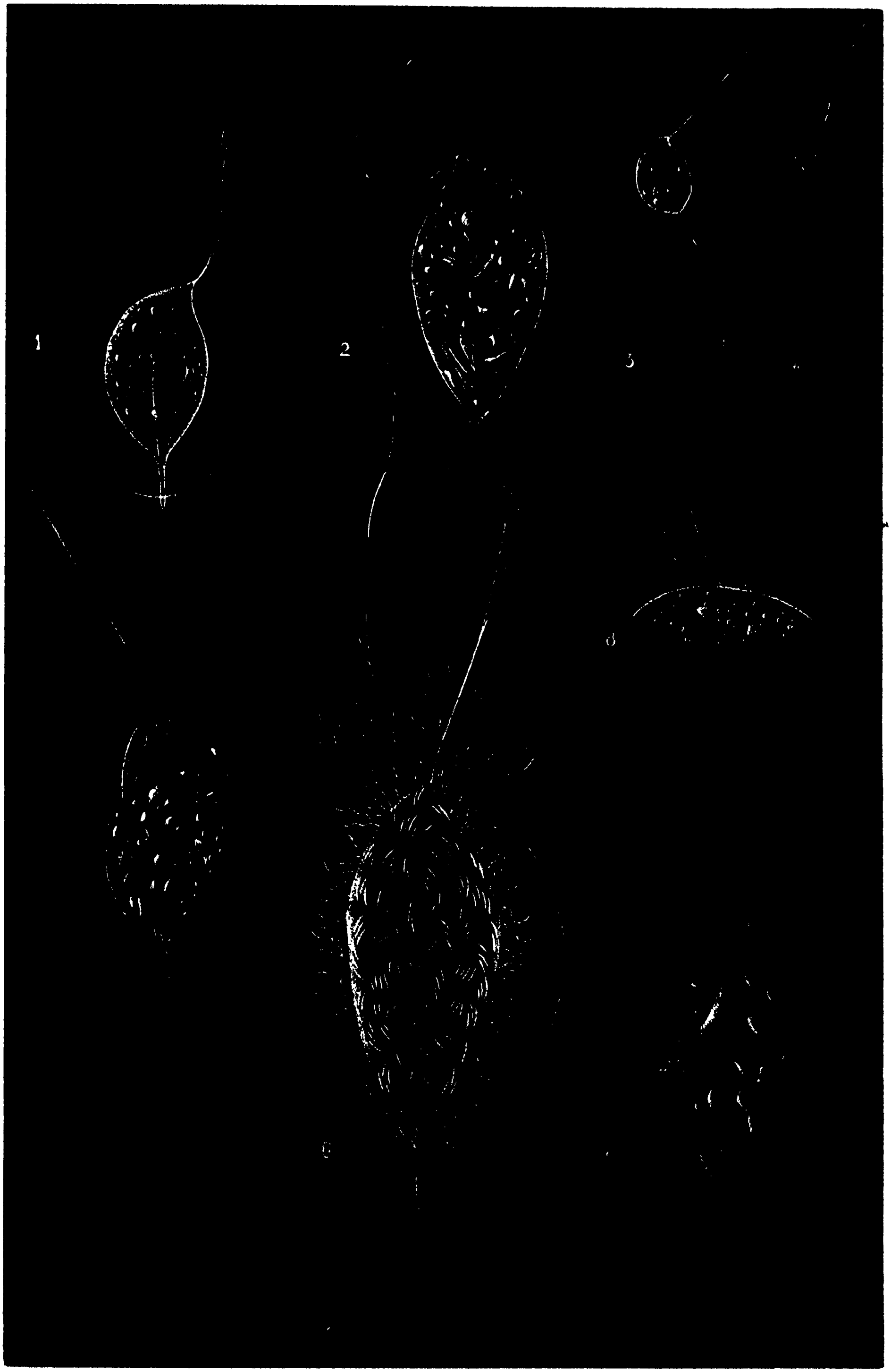
Figs. 3, 4. *Foaina exempla* Kirby from *Neotermes insularis.* Specimens of minimum size. × 1035.

Fig. 5. *Foaina costata* Kirby from *Neotermes insularis.* Specimen of maximum size. × 1035.

Fig. 6. *Foaina hilli* (Duboscq and Grassé) from *Glyptotermes iridipennis.* Spirochaetes (*Treponema hilli*) adherent to the entire surface, longer spirochaetes in the region of the papilla, short rods adherent full length to the surface of the body. × 1235.

Fig. 7. *Metadevescovina debilis* Light from *Kalotermes hubbardi,* showing adherent spirochaetes, with filamentous microörganisms on the caudal projection.

Fig. 8. A part of the body of *M. debilis,* showing adherent spirochaetes and among them filamentous microörganisms.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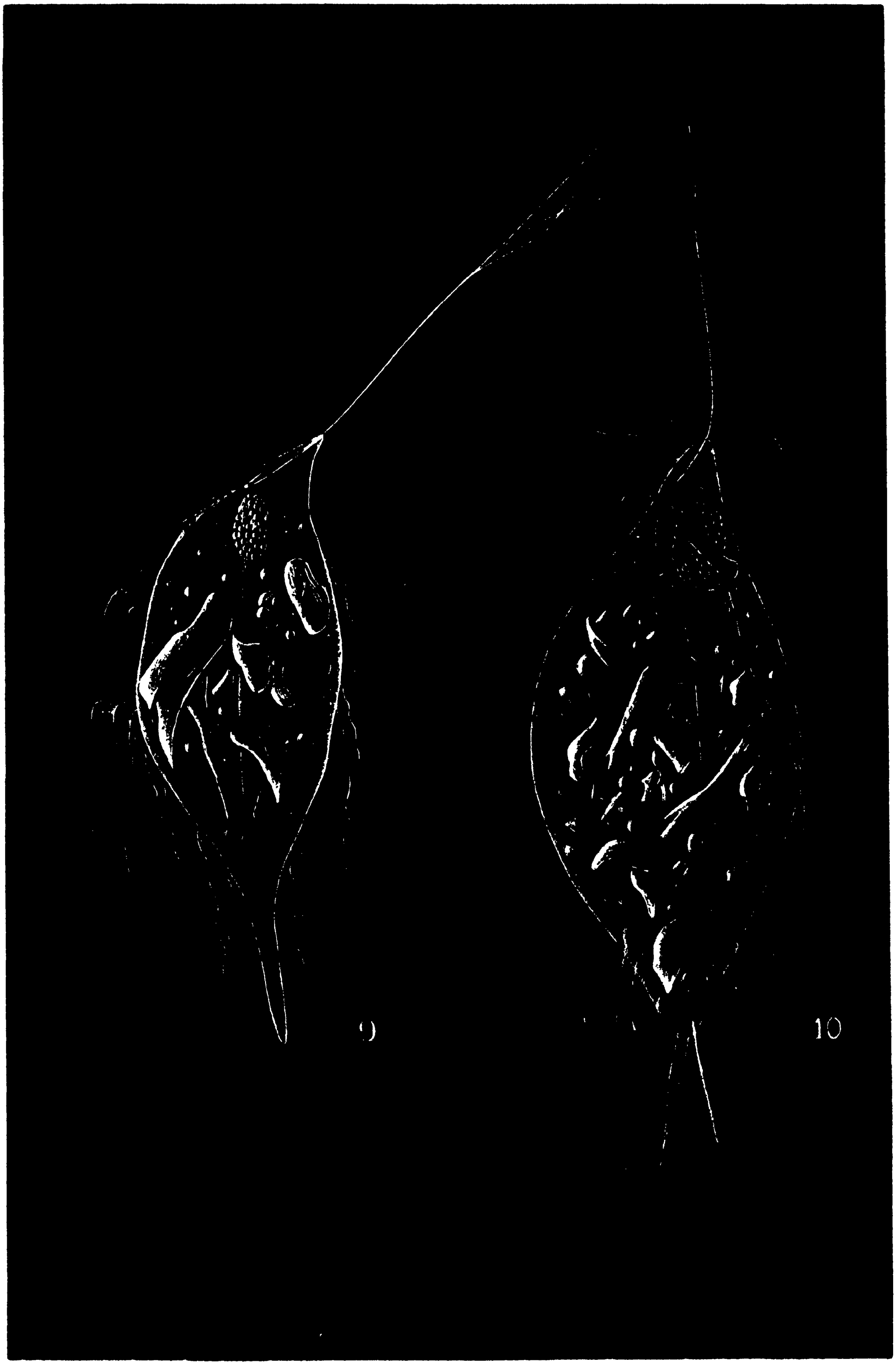
## PLATE 33

Drawings made from darkfield observations of living flagellates.

Fig. 9. *Devescovina lemniscata* Kirby from *Neotermes insularis*. Large specimen. A few stray spirochaetes are adherent to the body of this specimen, but there is no regularly adherent group. × 1354.

Fig. 10. *Metadevescovina cuspidata* sp. nov. from *Kalotermes minor*. Groups of spirochaetes adherent to the anterior and posterior ends are usually present on this species. × app. 2770.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# PLATE 34

Figs. 11–15. *Metadevescovina extranea* sp. nov. from *Mastotermes darwiniensis*. × 2440.

Figs. 11, 12. The axostyle is slender in this species, and the projection from the posterior end is characteristic. This projecting end is shown in fig. 12. S.H.

Fig. 13. The cresta is slender, and has a length of about 4$\mu$. Anterior to the nucleus is an expansion of part of the capitulum of the axostyle, and an extensive clear area. S.H.

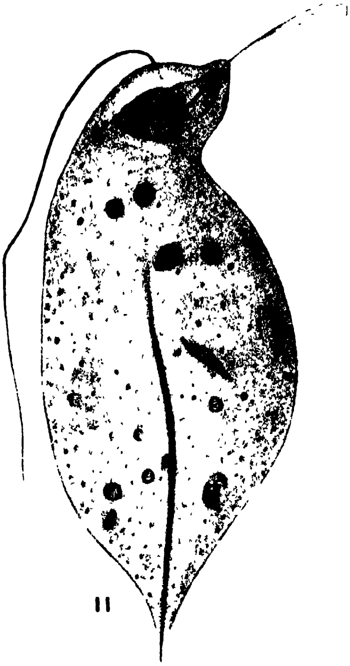
Figs. 14, 15. Parabasal body, relatively stout and turned around axostyle about one turn. Fl.R.

Figs. 16–17. *Metadevescovina modica* sp. nov. from *Kalotermes marginipennis*. S.H.F.

Fig. 16. The capitulum of the axostyle is moderately expanded, and the surface of the body is covered with spirochaetes. × 1770.

Fig. 17. Nucleus, capitulum and part of trunk of axostyle, and granules that are present on the capitulum of many specimens. × 2440.

Fig. 18. *Metadevescovina modesta* sp. nov. from *Glyptotermes angustus*. Characteristic of the species is the close spiral, with several turns, of the parabasal body. S.H. × 1770.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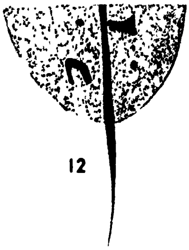
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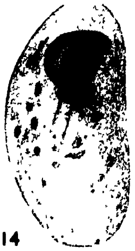
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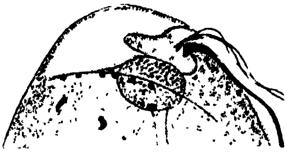
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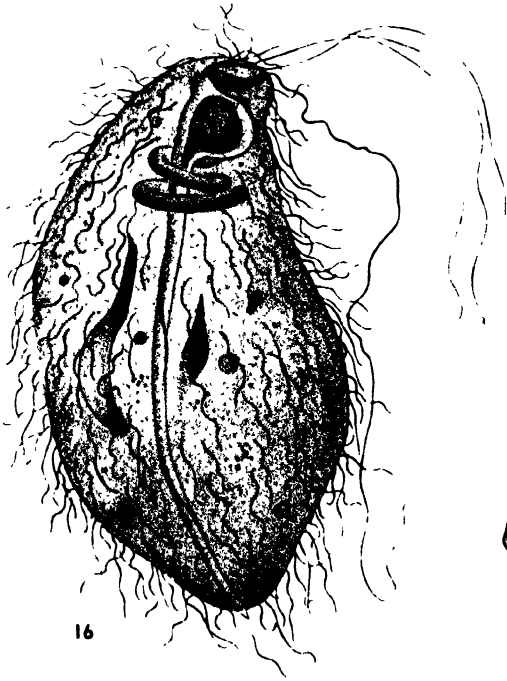
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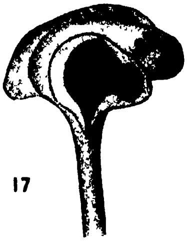
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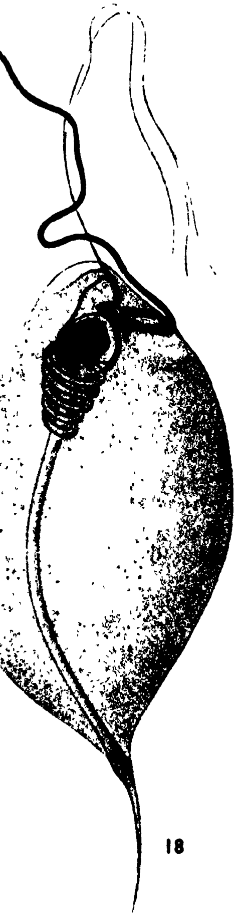
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# PLATE 35

*Metadevescovina stereociliata* (Grassi)

Fig. 19. From *Glyptotermes parvulus*. ? H. × 1770.

Figs. 20–24. From *Glyptotermes* sp. nov. T-2072. Uganda.

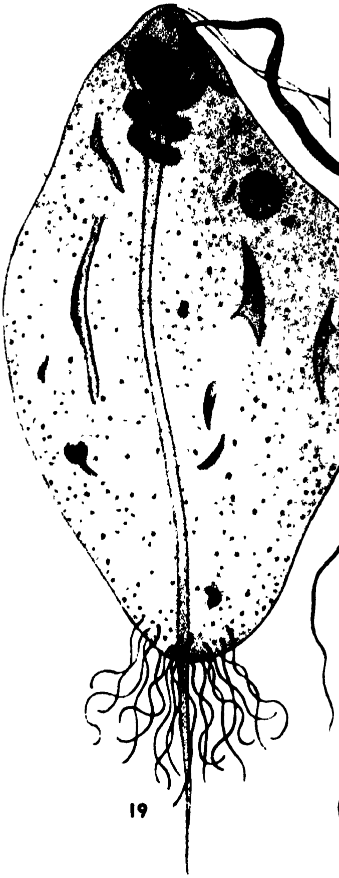
Fig. 20. Exterior view of stained specimen, showing the full length of the flagella, the long projection of the axostyle, and the group of spirochaetes adherent to the posterior end. The position of the trailing flagellum is altered for the purpose of the drawing. S.H. × 1175.

Fig. 21. Interior structure of the same specimen. × 2350.

Fig. 22. Structures of the anterior end, showing cresta, parabasal body with parabasal filament, and the anterior attachment of this filament, which leaves the other substance and parallels the anteromedial edge of the cresta. S.H. × 2350.

Fig. 23. Parabasal structure showing blocks of deep-staining substance alternating with clear bands, which in the posterior part are enclosed as vesicles. S.D. × 2350.

Fig. 24. Parabasal structure showing clear areas enclosed as vesicles by the stainable substance. S.D. × 2350.



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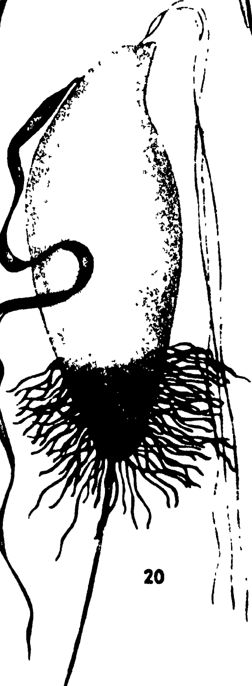

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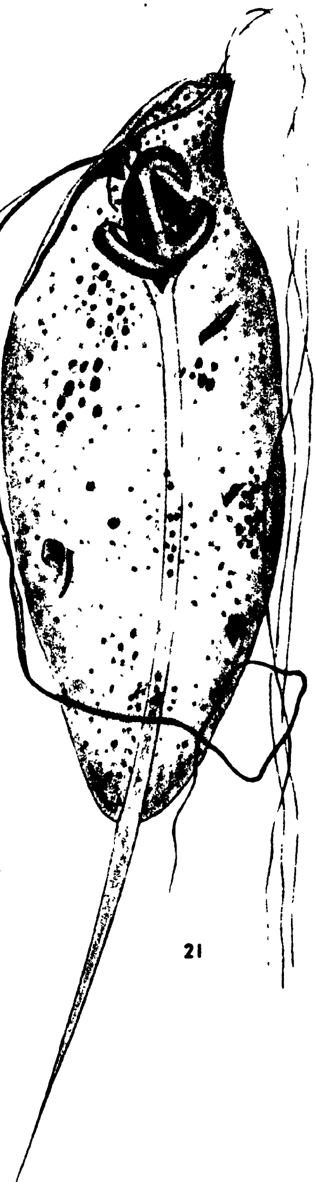

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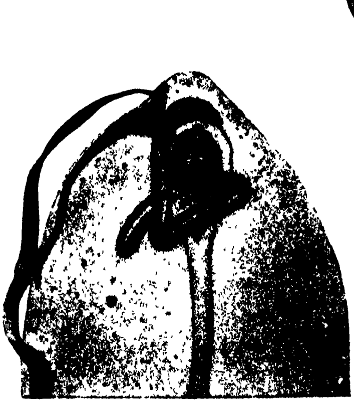

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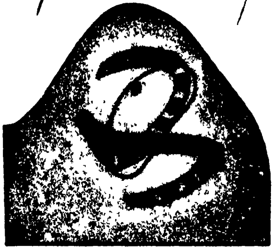

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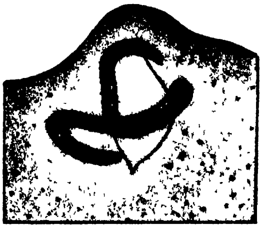

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## PLATE 36

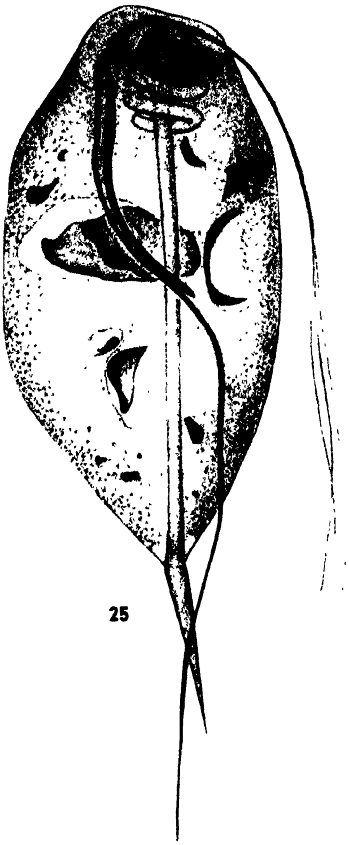
*Metadevescovina cuspidata* sp. nov. from *Kalotermes minor*

Figs. 25, 26. Specimens of large and of somewhat below average size. The spirochaetes adherent to the anterior and posterior ends are omitted. S.H. × 1770.

Figs. 27, 28. Details of the projecting cusp of the axostyle, optical section. In the second figure a few spirochaetes are adherent to the body. S.H. × 2440.

Fig. 29. Capitulum of axostyle observed from the left side. An elevated ridge, with chromatic granules, extends from the point where the trunk meets the capitulum to the region of the blepharoplast. This is represented in end view in figure 28. S.H. × 2440.

Fig. 30. Capitulum of axostyle observed from the dorsal aspect. S.H. × 2440.



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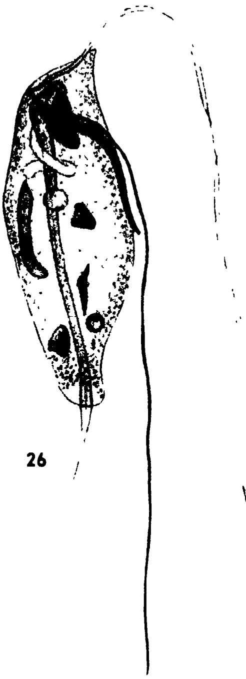

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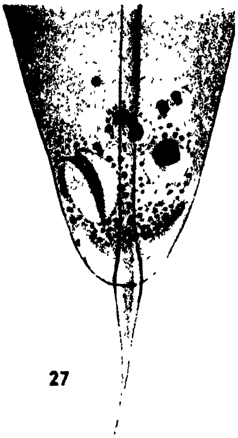

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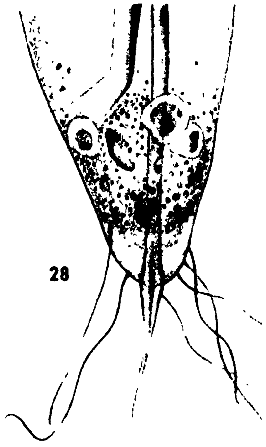

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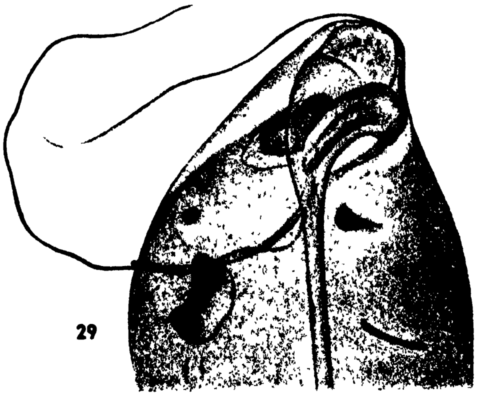

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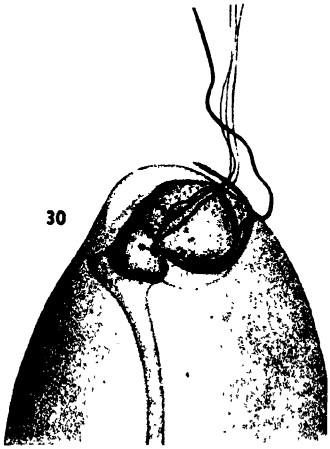

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# PLATE 37

Figs. 31–37. *Metadevescovina cuspidata* from *Kalotermes minor*

Fig. 31. The capitulum of the axostyle shows the posterior, spinelike extension on the ventral side and the lamella-like extension anterior to and paralleling the first loop of the parabasal body. S.H. × 2440.

Fig. 32. Capitulum of the axostyle from a different aspect, showing the origin of the narrow lamella-like structure that lies close to the first loop of the parabasal body. The parabasal filament is shown along the inner edge of the parabasal spiral. S.H. × 2440.

Fig. 33. Parabasal body showing two rows of granules. Saturated solution corrosive sublimate, Delafield. × 2440.

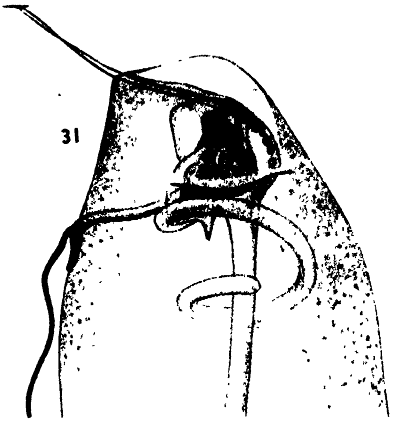
Fig. 34. Parabasal body with stained substance enclosing the clear areas as two rows of vesicles. S.D. × 3630.

Fig. 35. Parabasal body in a small individual, in which it is circular rather than oval in cross section, and there is a single row of granules. Saturated solution corrosive sublimate, Delafield. × 2440.

Fig. 36. Parabasal body showing two rows of granules in its posterior part. Saturated solution corrosive sublimate, Delafield. × 2440.

Fig. 37. Parabasal body with one ramus, which also contains two rows of granules. Saturated solution corrosive sublimate, Delafield. × 2440.

Fig. 38. *Metadevescovina cristata* sp. nov. from *Neotermes* sp. nov. T-1040. Fl.H. × 1710.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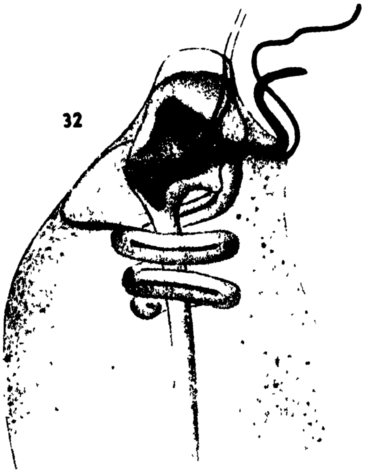
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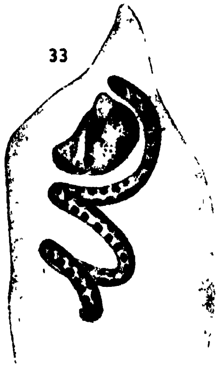
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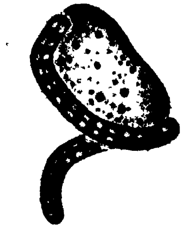
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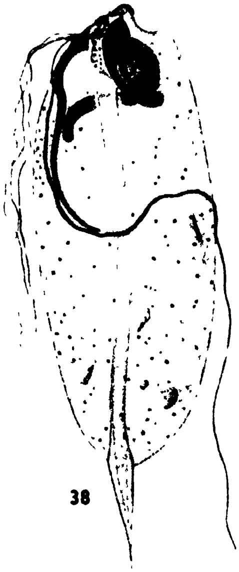
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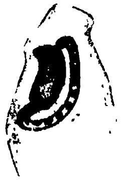
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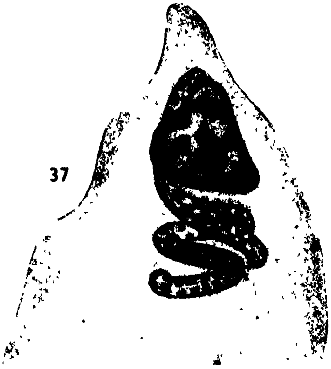
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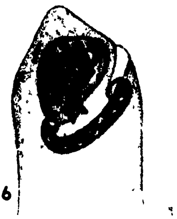
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## PLATE 38

*Metadevescovina patula* sp. nov. from *Kalotermes condonensis*

Fig. 39. Exterior view showing spirochaetes adherent to the anterior and posterior ends. Fl.H. × 1146.

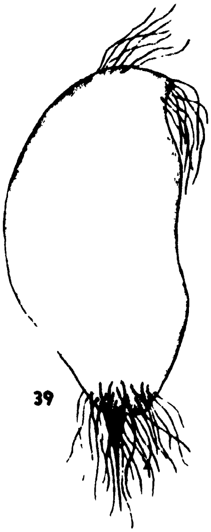
Fig. 40. Characteristic of the species is the stemlike connection alongside the nucleus between the anterior and posterior sections of the parabasal body. S.H. × 2270.

Fig. 41. Blepharoplast aggregate with attachment of the cresta and the parabasal filament, which runs along one edge of the whole parabasal body except the anterior section. Fl.H. × 2270.

Fig. 42. The blepharoplast appears as an aggregate of granules; the nucleus is elongated transversely and curved; the capitulum lies on the left side of the nucleus—above it as represented in this figure. Fl.H. × 2270.

Figs. 43, 44. Relationship of the parabasal body to the nucleus and the slender connection between the anterior and posterior sections of the parabasal. The curved shape of the nucleus is represented in fig. 44. Fl.H. × 2270.

Fig. 45. The cytoplasm contains numerous fragments of wood and small flagellates. S.H. × 1770.



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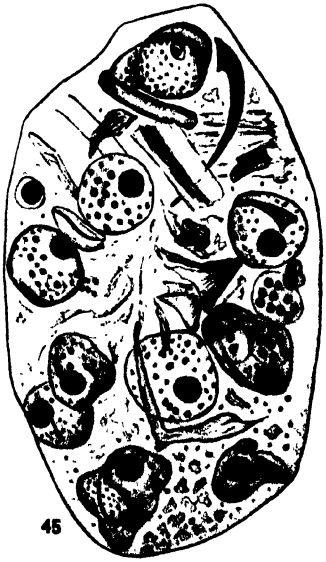

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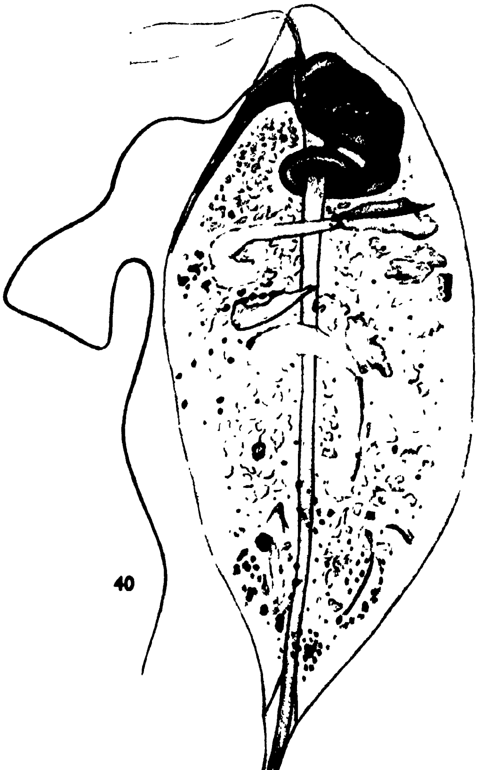

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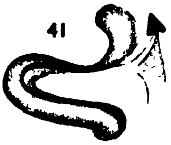

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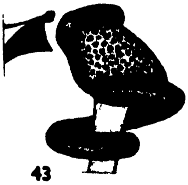

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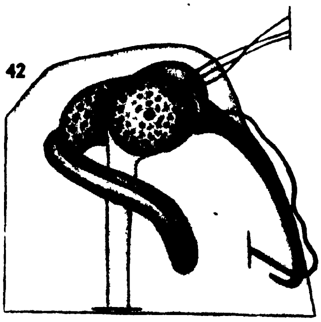

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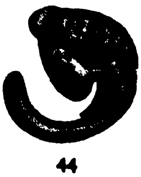

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## PLATE 39

Figs. 46–48. *Metadevescovina turbula* sp. nov. from
*Kalotermes jouteli.* × 2270.

Fig. 46. Adherent spirochaetes are abundant on the surface of the body, and there are also adherent rods and filaments, but all these microörganisms are omitted from the figure. Holl.H.

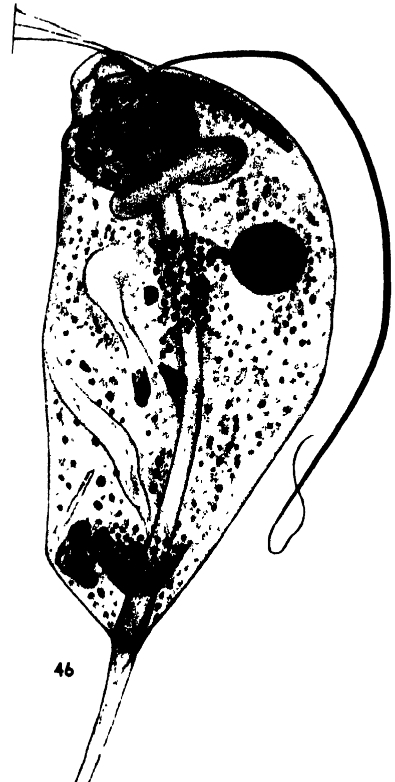
Figs. 47–48. Aggregate of rods and granules around the anterior part of the trunk of the axostyle. C.H.

Fig. 49. *Metadevescovina nudula* sp. nov. from *Kalotermes jouteli.* No adherent microörganisms are present. C.H. × 2270.

Figs. 50–52. *Metadevescovina fulleri* from *Kalotermes durbanensis.*

Figs. 50, 51. Adherent spirochaetes more restricted to certain areas of the body in one specimen than in the other. S.H., Fl.R. × 1160.

Fig. 52. Adherent spirochaetes not shown. S.H. × 1710.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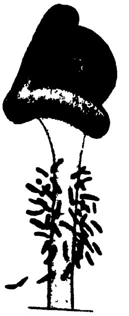
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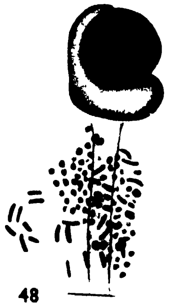
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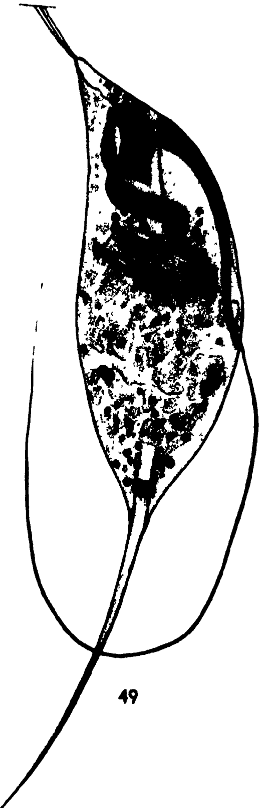
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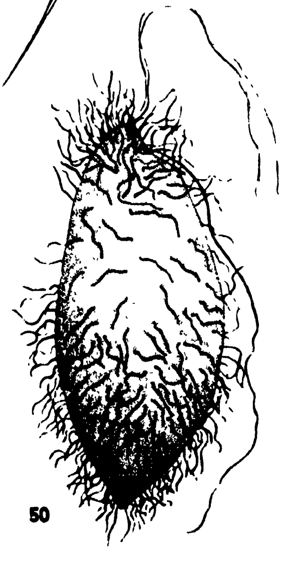
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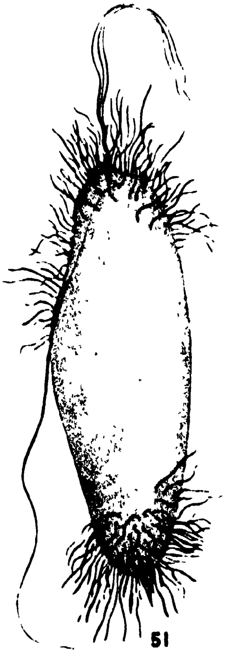
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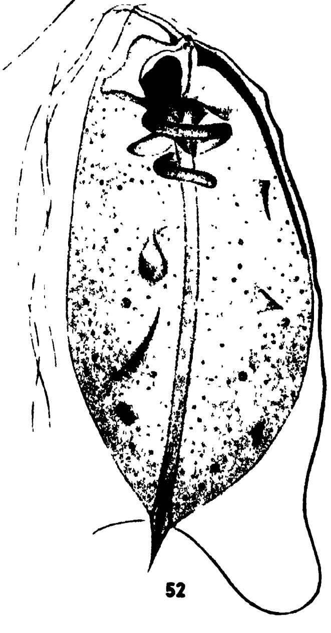
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# PLATE 40

Fig. 53. *Metadevescovina fulleri* sp. nov. from *Kalotermes durbanensis.* Adherent spirochaetes omitted. The membranous expansion of the capitulum of the axostyle is shown. S.H. × 1710.

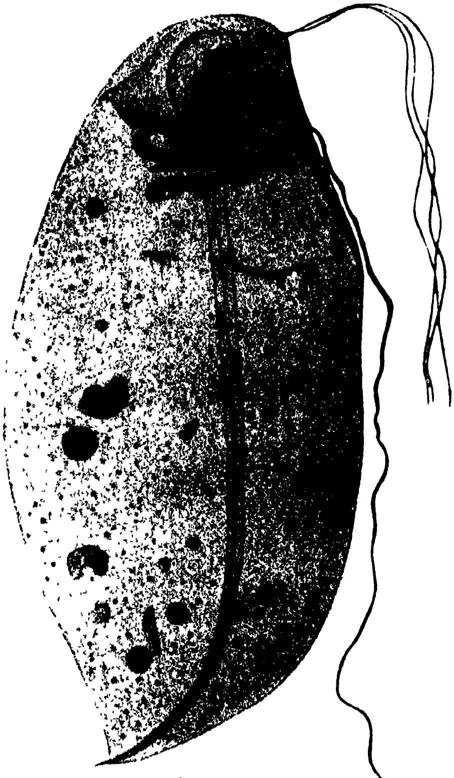
Figs. 54–59. *Metadevescovina carina* sp. nov. from *Kalotermes madagascariensis.* × 2330.

Fig. 54. No adherent microörganisms are present. Characteristic of the species is the long, broad cresta; and the long gap alongside the nucleus between the anterior and posterior sections of the parabasal body. Fl.R.

Fig. 55. A flagellate of much smaller size, with the cresta reaching nearly to the posterior end, and a large projecting cusp. Holl.H.

Figs. 56, 57. Cresta nucleus, trailing flagellum, and parabasal body, showing the two sections of the parabasal body, and the filament from the posterior section passing directly to the blepharoplast, paralleling the anteromedial edge of the cresta. Fl.R.

Figs. 58, 59. Specimens, differently stained, showing the gap between the two sections of the parabasal body. S.D.



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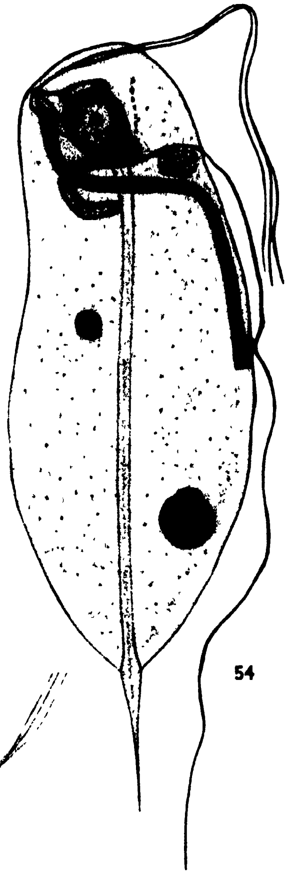

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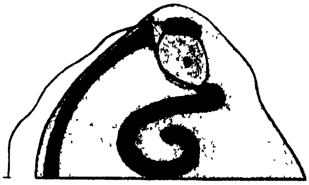

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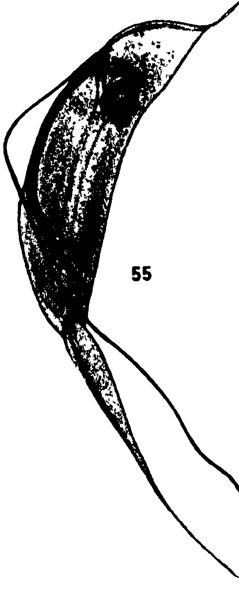

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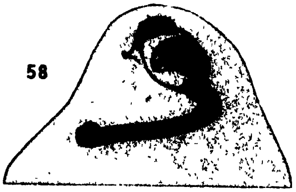

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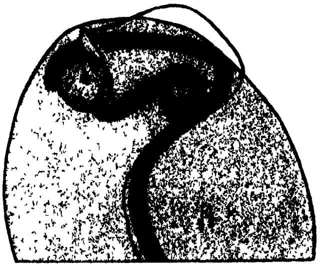

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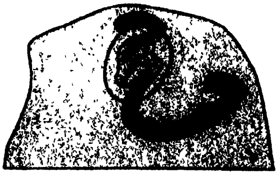

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# PLATE 41

Fig. 60. *Metadevescovina nitida* sp. nov. from *Procryptotermes paradoxus*. The capitulum of the axostyle is extended in a spiral membrane which is followed by the parabasal body. Fl.R. × 2330.

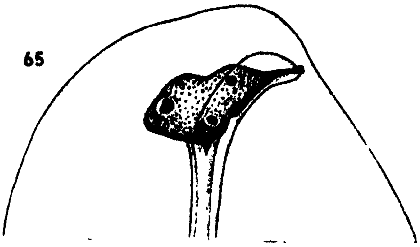
Figs. 61–65. *Metadevescovina debilis* Light from *Kalotermes hubbardi.*

Figs. 61, 62. Whole specimens with spirochaetes omitted. The expanded capitulum of the axostyle is shown. There is a group of four granules in the blepharoplast complex, and the cresta, as shown in fig. 62, is small in this species. S.H. × 1770.

Fig. 63. Detail of the expanded capitulum of the axostyle on the right side of the nucleus, the membrane forming a trough in which the anterior part of the parabasal body is situated. S.H. × 2400.

Fig. 64. Irregular shape of the nucleus, which is surrounded by the capitular membrane, and four granules in the blepharoplast complex. The core of the axostyle meets the posterior end of the nucleus. S.D. × 2400.

Fig. 65. Irregular shape of nucleus, with tapering extension toward the blepharoplast. Three nucleoli are present in the nucleus. The manner in which the trunk of the axostyle meets the nucleus is shown. Compare fig. 62 for relation to the capitular membrane. S.D. × 2400.



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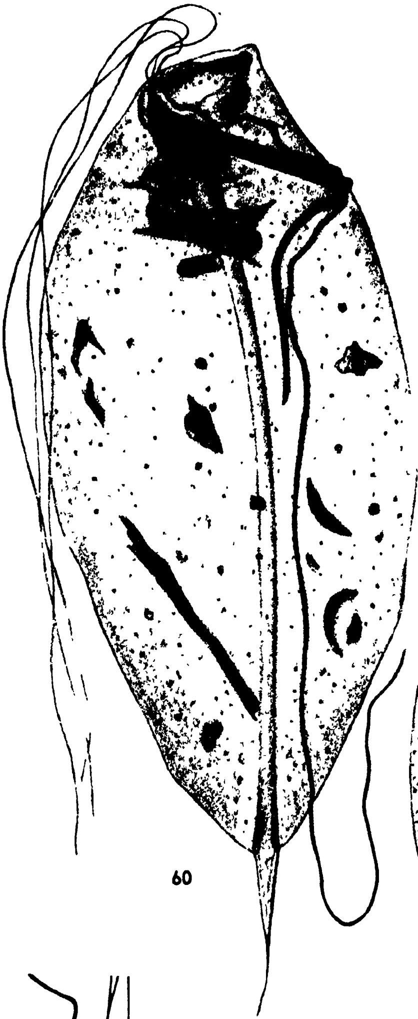

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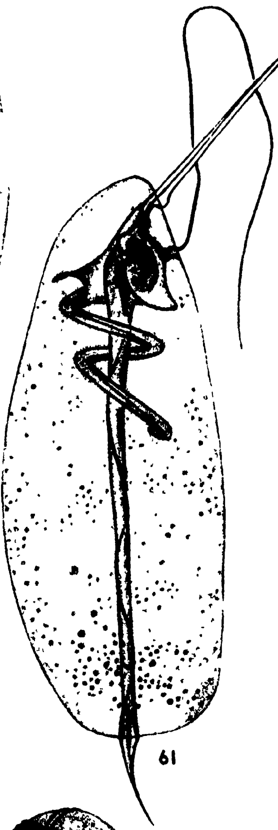

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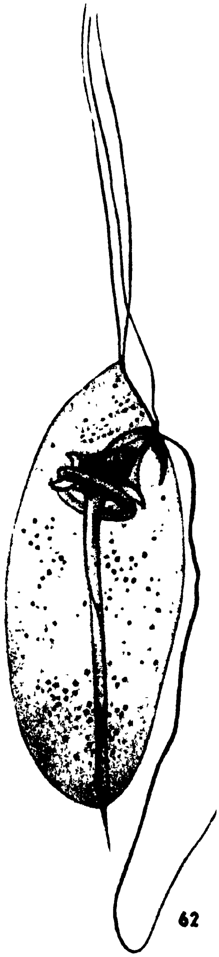

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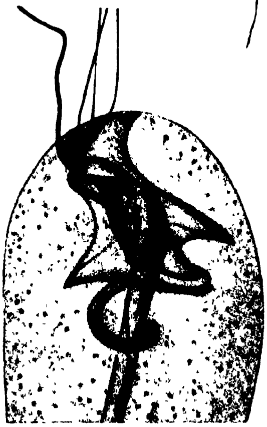

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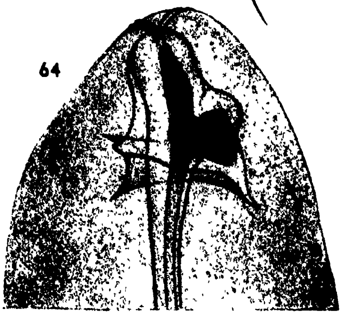

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## PLATE 42

Figs. 66–70. *Metadevescovina debilis* from *Kalotermes hubbardi*

Fig. 66. Left side of the capitulum of the axostyle and its relation to the parabasal body. S.H. × 2400.

Fig. 67. Parabasal body with heterogeneous structure of alternating stained and unstained discs. S.D. × 2400.

Fig. 68. Parabasal body with one long ramus. S.D. × 1770.

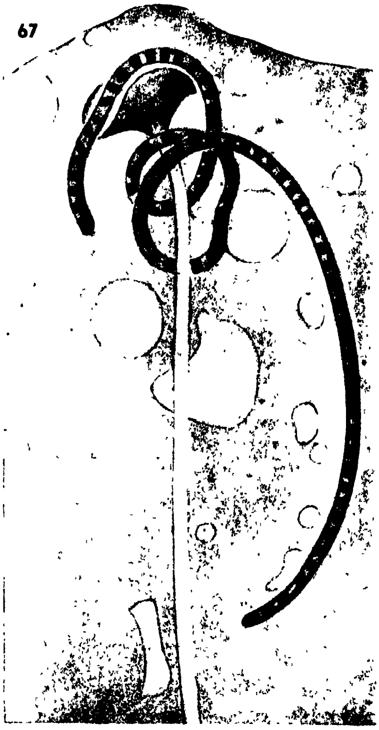
Fig. 69. Another parabasal body with a long ramus.

Fig. 70. Oval bodies in outer layer of cytoplasm. These were especially numerous in this specimen. There were a few in many others in the same preparation, not present in the deeper cytoplasm. Osmic vapor killed, Janus green.

Figs. 71–72. *Metadevescovina polyspira* (Lewis) from
*Kalotermes occidentis*

Fig. 71. Specimen of average size. Parabasal body unbranched, as in the majority of the flagellates of the species. Adherent spirochaetes are present, but are not shown. × 1770.

Fig. 72. Rodlike microörganisms present on the surface of the body. Parabasal body and cresta. × 2400.



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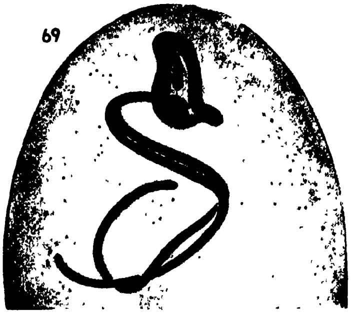

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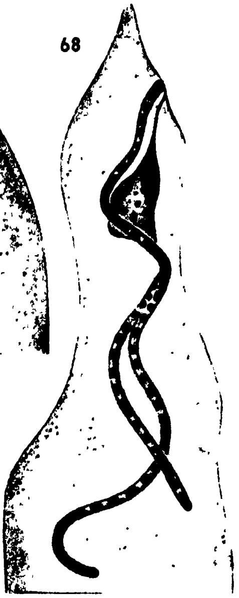

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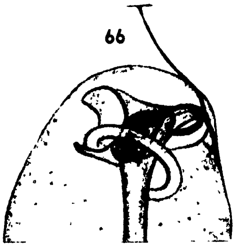

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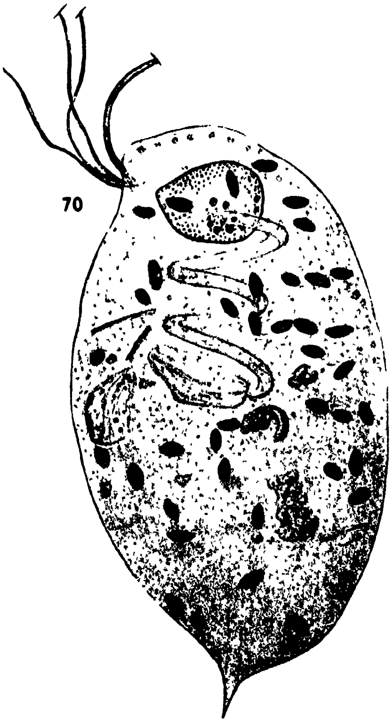

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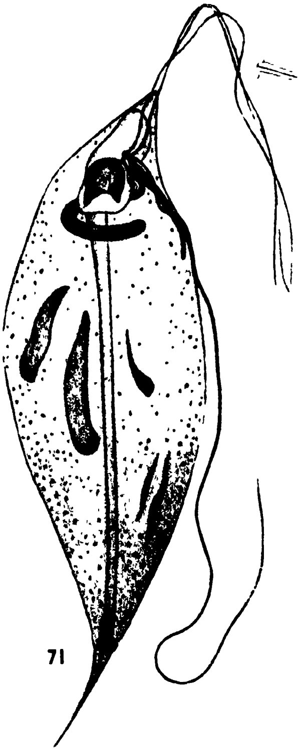

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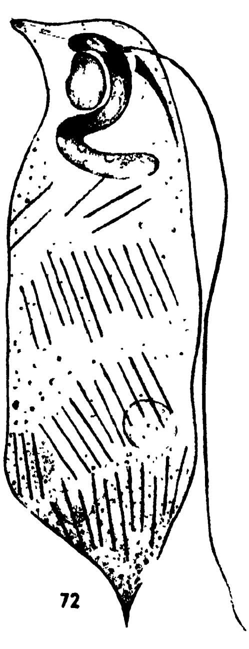

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# PLATE 43

Figs. 73–74. *Metadevescovina polyspira* (Lewis) from
*Kalotermes occidentis*

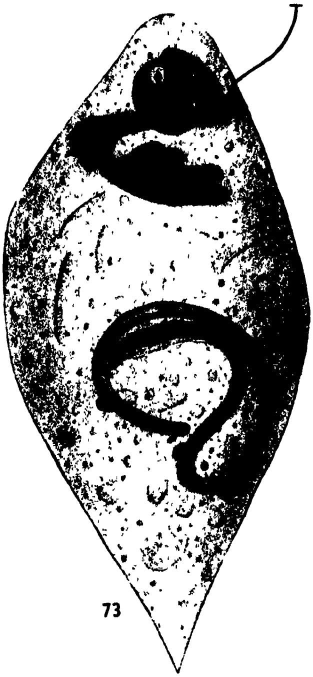
Fig. 73. Branched parabasal body, which is present in most large specimens. × 1770.

Fig. 74. Telophase of division, with each parabasal body bearing several rami. × 2440.

Figs. 75–76. *Metadevescovina magna* sp. nov. from
*Kalotermes marginipennis*. S.H.

Fig. 75. Spirochaetes covering the body, with a group of especially stout ones at the posterior end, and a line of spirochaetes in the region of the transverse membranous extension of the axostyle. × 1175.

Fig. 76. Same specimen, internal structure in more detail. The capitulum of the axostyle is extended in a long, narrow, spiraled membrane, the inner surface of which is followed by the parabasal body. The spiral filament around the trunk of the axostyle may be a remnant of the paradesmose. × 1770.



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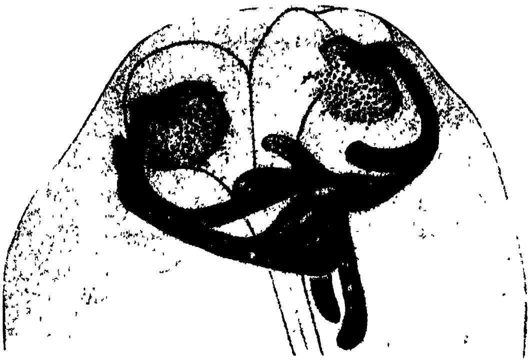

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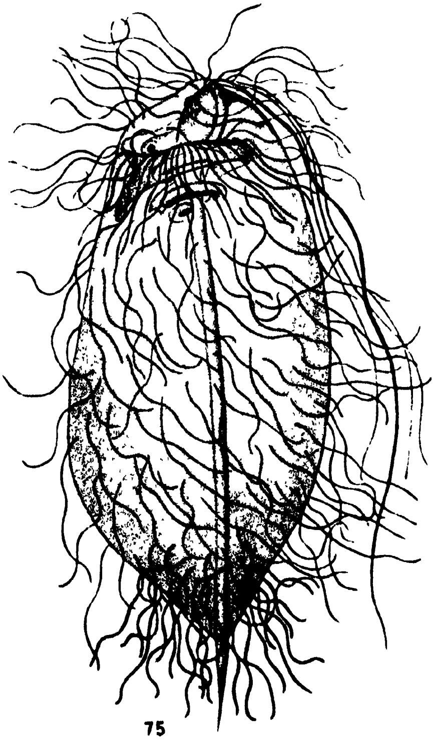

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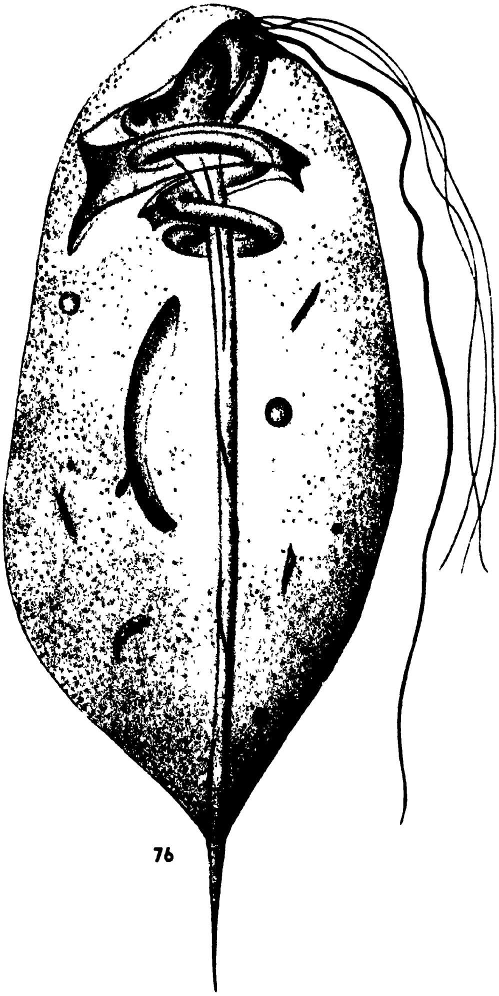

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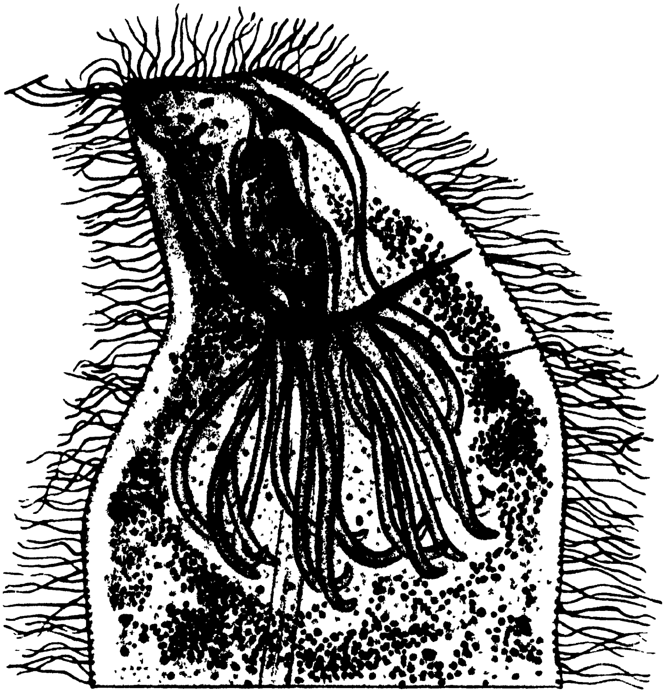
# PLATE 44

Fig. 77. *Pseudodevescovina uniflagellata* Sutherland. Anterior part of body. Only the proximal parts of the three anterior flagella are shown. The parabasal apparatus consists of a main limb that passes longitudinally alongside the nucleus, then transversely; and a number of cords attached to the transverse part. From the capitulum in the papilla there extends posteriad a cylindrical appendage, which comes in contact with the parabasal body at the bend. Spirochaetes cover the surface, and in the cytoplasm at the end of each spirochaete is a granule. S.H. × 2330.

Fig. 78. *Pseudodevescovina ramosa* Kirby. The capitulum of the axostyle is moderately expanded in membranous extensions. The parabasal apparatus consists of a proximal part and an attached ramus system. The proximal part is turned in a short hook at its anterior end, extends longitudinally alongside the nucleus, turns anteriorly, in a U-form, then extends transversely to the edge of the body. At the bend of the U are attached the main stems of the ramus system. These branch in a number of cords, which lie transversely and are turned around the axostyle. This turning, however, is not equivalent to the spiral of the parabasal body of *Devescovina*, *Metadevescovina*, and other genera. The cresta is small. The surface of the body is covered with spirochaetes. Fl.R. × 2280.



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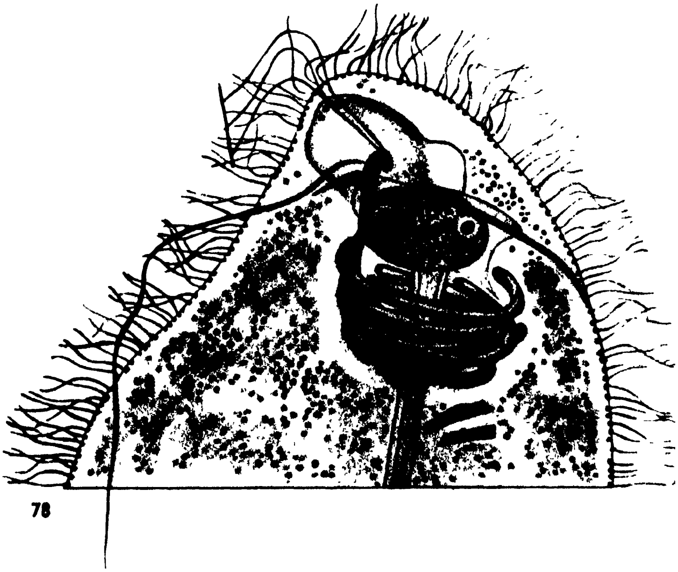

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# DEVESCOVINID FLAGELLATES OF TERMITES

# V. THE GENUS HYPERDEVESCOVINA, THE GENUS BULLANYMPHA, AND UNDESCRIBED OR UNRECORDED SPECIES

BY

HAROLD KIRBY

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# DEVESCOVINID FLAGELLATES OF TERMITES

## V. THE GENUS HYPERDEVESCOVINA, THE GENUS BULLANYMPHA, AND UNDESCRIBED OR UNRECORDED SPECIES

BY

HAROLD KIRBY

◆

## INTRODUCTION

WITH REFERENCE to the material used and the aid given in the preparation of this article, there should be acknowledgment additional to that made in the first paper of the series.

The greater part of the preparations of species of the genus *Hyperdevescovina* were made by Professor L. R. Cleveland in New Zealand and Australia. The descriptions and records of undescribed or unrecorded species are derived from material originating in British Guiana and El Salvador. The collection from British Guiana was obtained by Professor Alfred E. Emerson and delivered to the late Professor C. A. Kofoid. The termite hosts were described by Emerson (1925). Professor Kofoid studied several of the devescovinids, as well as other flagellates; he prepared illustrations of them; and he included them in the subject matter of a lecture, "Parasitism and Evolution," given at a meeting of the National Academy of Sciences in 1923. His manuscript, which did not go into detail concerning the organization of the flagellates, was not published. While I was preparing this part of the monograph on devescovinid flagellates, Professor Kofoid gave me the slides made from termites from British Guiana. The collection from El Salvador was made by Dr. Joe T. Marshall, while he was on an expedition related to the work of the Museum of Vertebrate Zoölogy. He also secured specimens of the termite hosts, which are now in Professor Emerson's collection.

Professor Emerson gave me the names of the termites referred to in this paper, including revisions that he has made but has not yet published, and generously permitted me to use the information. It should be emphasized that he is to be credited with all the nomenclatorial matters concerning the termites.

Assistance in the study of the material and the preparation of the illustrations was recently given by Mr. Bronislaw Honigberg and Mrs. Lois G. Taylor. Financial aid was provided by the Research Committee of the University of California and the Penrose Fund of the American Philosophical Society.

# DESCRIPTIVE AND SYSTEMATIC ACCOUNT

## GENUS HYPERDEVESCOVINA KIRBY

### **Hyperdevescovina** Kirby

*Hyperdevescovina* Kirby, 1947, J. Parasit., 33:225; type species *calotermitis* Nurse (*Caduceia calotermidis* Nurse).

*Diagnosis.*—Body broad at anterior and posterior ends; average length in known species 46–78μ, range 33–139μ; average width 30–51μ, range 19–78μ; three long, slender anterior flagella; trailing flagellum moderately slender, usually shorter than body; cresta very small, two sides diverging from apex equal, excavated posteriorly; parabasal body without longitudinal proximal part, turned around axostyle 2–19 times, usually simple, occasionally with short ramus that spirals with the rest; capitulum of axostyle often extended in pennant-shaped or cape-formed membrane, over which short rods are present in most species; trunk of axostyle stout, slender posterior projecting end, with length from a few microns to nearly as much as rest of body; nucleus usually ellipsoidal in form, longer axis longitudinal or oblique, abundance of more or less coarsely granular, deep-staining material in chromatic mass, with peripheral nucleolus; belt of peripheral rods present in most species in peripheral cytoplasm of middle and posterior parts of body; spirochaetes usually adherent to posterior end and in some species also to anterior end.

#### TAXONOMY AND DISTRIBUTION

The flagellate that I have designated as type species of this genus was placed by Nurse (1945) in the genus *Caduceia,* and named *Caduceia calotermidis.*

*Hyperdevescovina* is similar in many respects to *Caduceia,* but I have differentiated it chiefly because of two features. One is the unique type of cresta, which is uniform throughout the genus and differs markedly from that of all other known devescovinids. The other feature is the trunk of the axostyle, which does not, as in *Caduceia,* taper to a filamentous posterior part enclosed in the cytoplasm, but is stout and projects from the cytosome in a spikelike terminal part. This difference in the axostyles is of the same character as that between *Devescovina* and *Metadevescovina.*

Species of *Hyperdevescovina* occur in termites of Australia, in which there are several, and in one termite each of Ceylon, South Africa, and New Zealand. I have seen no species in any termite examined from North, Central, or South America, in any termite of Africa except the one named, or in hosts from Madagascar, Java, or Sumatra.

Eight of the host species occur in the Australian Region. In the monograph by Hill (1942), seven of them are placed in the genus *Calotermes,* without assignment to a subgenus. As given by Hill, the names of these are: *Calotermes* (subgen. ?) *brouni* Froggatt, *C.* (subgen. ?) *obscurus* (Walker), *C.* (subgen. ?) *rufinotum* Hill, *C.* (subgen. ?) *spoliator* Hill, *C.* (subgen. ?) *tillyardi* Hill, *C.* (subgen. ?) *banksiae* Hill, and *C.* (subgen. ?) *pallidinotum* Hill. The eighth Australian host is placed by Hill in *Cryptotermes,* as *Calotermes* (*Cryptotermes*) *atratus* Hill. The Ceylon host is *Neotermes militaris* (Desneux). In South Africa the host is a termite that has been recognized by Professor Emerson as a new species.

Professor Emerson has informed me that all the termites that are hosts of *Hyperdevescovina,* except *Neotermes militaris,* belong to a new genus, to which he has given the name *Proglyptotermes.* The new genus is intermediate between *Neotermes* and *Glyptotermes*. The manner in which he has related the hosts to one another brings a greater degree of regularity than was previously apparent into the distribution pattern of species of *Hyperdevescovina*.

The names supplied by Professor Emerson, all of which at the time of writing had not been published, are as follows:

*Proglyptotermes hilli* Emerson for *Kalotermes obscurus* (Walker). Emerson requested me to add to this name the following statement, of which he is the author: "Emerson (MS) has designated this species as the generitype of the genus *Proglyptotermes*. The specific name *P. hilli* is proposed for *Calotermes* (subg. ?) *obscurus* described and figured by Hill, 1942, pp. 105–107, figs. 53, 54. Walker, 1853, p. 527, described the imago of this species under the name *Termes obscurus*. Walker's name was preoccupied by *Termes* (*Eutermes*) *obscurus* Heer, 1849, p. 33, Pl. 3, fig. 4, a fossil termite from the lower Miocene at Radoboj, Croatia, so far not placed in any recognized genus within the modern system of classification."

*Proglyptotermes brouni* (Froggatt) for *K. brouni*.

*Proglyptotermes pallidinotum* (Hill) for *K. pallidinotum*.

*Proglyptotermes tillyardi* (Hill) for *K. tillyardi*.

*Proglyptotermes atratus* (Hill) for *Cryptotermes atratus*.

*Proglyptotermes spoliator* (Hill) for *K. spoliator*.

*Proglyptotermes rufinotum* (Hill) for *K. rufinotum*.

*Proglyptotermes banksiae* (Hill) for *K. banksiae*.

*Proglyptotermes* sp. nov. This is the species obtained from South Africa.

All the new combinations are to be ascribed to Emerson.

Six of the eight species of *Hyperdevescovina* occur each in one host termite. The other two species have two hosts each. These are *Hyperdevescovina mitrata* in *Proglyptotermes pallidinotum* and *P. tillyardi*, and *H. falcifera* in *P. rufinotum* and *P. banksiae*. The differences between species are not always very large, but they are definite. The genus *Hyperdevescovina* seems in general to have undergone pronounced differentiation in different hosts.

In all the termites that contain *Hyperdevescovina*, the type of flagellate faunule is similar. *Hyperdevescovina* is the only devescovinid—a fact that is significant in connection with the supposed existence of life cycles made up of forms that differ markedly in morphology (Kirby, 1941, p. 14). Changes in form and size of the sort that are supposed to exist in certain species, but which actually represent different species, certainly are not indicated in *Hyperdevescovina*. *Trichonympha* is present in some of the host species but not in others; and in this group of termites it is always of the *T. chattoni* type. Two species have been considered to be different from *T. chattoni* on the basis of minor features: *T. zeylanica* (Dobell) in *Neotermes militaris* and *Proglyptotermes hilli*, and *T. divexa* Kirby in *Proglyptotermes* sp. nov. of South Africa. These termites contain no large flagellates except *Hyperdevescovina* and *Trichonympha*. The other flagellates of the faunules are oxymonads and *Tricercomitus*, which are widely distributed in termites of the family Kalotermitidae; and a small undescribed hypermastigote that occurs in *P. banksiae* and *P. rufinotum*.

## GENERAL MORPHOLOGY

In size and shape the species of *Hyperdevescovina* are similar to those of *Caduceia* and *Pseudodevescovina.* They are among the largest devescovinids. The smallest species has an average length of somewhat more than half that of the largest species, and within most species the individual range in length is somewhat more or less than one to two. Almost the entire range of length in the genus is present, however, within the one species *H. caudata.*

A relatively small papilla is present at the anterior end; in living specimens of *H. mitrata* it was observed that this structure moves together with the whip of three anterior flagella. In relation to the size of the body, it is much less prominent than the papilla of *Devescovina.*

*Hyperdevescovina* has three long and slender anterior flagella, as in all devescovinids. Their length comes close to equaling the length of the body, except when that is unusually short or exceptionally long. The trailing flagellum has similar characteristics in all species. It is much stouter than an anterior flagellum in its thicker part and is slender in its anterior and posterior parts. Sometimes the trailing flagellum is about equal to the body in length, but usually falls short of this. In *Hyperdevescovina* its development in relation to body size is similar to that in *Caduceia.*

In the type species, Nurse reported a single blepharoplast to which the flagella connect, but actually this and other species have no single granule of this nature. It is, in fact, not possible to speak of a single blepharoplast in which all mastigont structures meet directly. There is a complex of endings and interconnections where the mastigont structures come together. The structural details of the complex have been observed only in certain favorable preparations, which did not include all the species. In the material in which it has been studied, the complex is, in general, uniform, and this is probably true of the genus as a whole. The complex is similar to that of *Macrotrichomonas pulchra,* which was described by Kirby (1942, p. 117).

The anterior flagella terminate in two roots that end separately; at a distance from the two ends, also in line with them, is the cresta. The position of the cresta may be considered to be dorsal, and the two roots of the flagella may be referred to as dorsal and ventral. In the examination of many specimens it is possible to be certain that two flagella meet in the dorsal root (pl. 50, fig. 31). In other specimens it may be the ventral root that divides; occasionally that appeared to be true (pl. 45, figs. 2, 6). In *Macrotrichomonas pulchra* it is the dorsal root that divides. The proximal parts of the flagella are usually not so stout in *Hyperdevescovina* as they are in *M. pulchra,* but the ventral root often shows an enlargement at its proximal end. The dorsal flagellar root ends at a small granule to which other structures also connect, and if any granule is to be considered the single center of the mastigont organization it would be this one. Extending posteriorly from the granule-complex is a larger, deep-staining body that is generally elongate and often irregular in shape (pl. 50, fig. 31; pl. 45, fig. 5). A similar body is present in *M. pulchra.*

The apex of the cresta lies a short distance from the small central granule, and probably is connected to it by a fine filament. The trailing flagellum follows the outer edge of the cresta, and apparently terminates in the granule at the place closest to the apex of the cresta (pl. 50, fig. 31). Near the cresta is a curved rod (pl. 45, figs. 4–6; pl. 53, fig. 47), which I have seen in several species. Along the inner edge of the cresta is a filament (pl. 49, fig. 25; pl. 50, fig. 31) that passes posteriorly, turns transversely, and extends for a short distance along the posterior edge of the parabasal body in its first gyre. This filament has been termed in this paper the "accessory filament"; it is homologous with the structure that was called the "paracrestal filament" in *Macrotrichomonas pulchra,* and the "crestal accessory" in *Caduceia monile.* The structure is enlarged in some species, and in *H. calotermitis* it is often band-shaped (pl. 45, figs. 4–6). It was considered by Nurse to be the parabasal thread, but the parabasal filament is a different structure. *Hyperdevescovina caudata* shows more clearly than other species that the two structures are separate; in many specimens, at least, the accessory filament of that species does not come into contact with the parabasal body, and a parabasal filament can also be seen (pl. 50, fig. 29).

The cresta is similar in shape and size throughout the genus *Hyperdevescovina,* and the shape differs from that in other devescovinids. The cresta was not seen by Nurse in the original description of the type species, and he stated incorrectly that it is absent. In devescovinids of other genera the cresta is longest in the external edge, shorter in the posteromedial edge, and shortest in the anteromedial edge; the angle that meets the center of the mastigont organization is between the shortest and longest edge. The cresta in *Hyperdevescovina* (pl. 49, fig. 26) is very small, and the apical angle is between two edges of equal length. The length of these edges is about 1.5–3$\mu$, and the angle between them is sometimes 90° and sometimes greater. Opposite the apical angle the edge is incurved more or less deeply. This edge is comparable to the posteromedial edge of the usual devescovinid cresta, but in *Hyperdevescovina* it is posterior and not medial. It is usually a definite edge, concave in form; but some crestas have a sharp inner angle, so that no single edge exists and the cresta seems formed of two narrow, diverging arms.

The nuclear rhizoplast is usually a rather inconspicuous structure. It is straight or bent in its course, and in at least some species it turns and runs along the surface of the nuclear membrane for a certain distance after it meets that structure. In *H. calotermitis* it is sometimes broadened to a band (pl. 45, fig. 3).

In all the species of *Hyperdevescovina* that I have studied, the parabasal body is turned in a closely wound helix around the trunk of the axostyle and usually also around the posterior part of the nucleus (pl. 49, fig. 27). The most distinctive feature of the parabasal body in the genus is the absence of a longitudinal part of the main substance. There is a space between the proximal end of that substance and the anterior granule-complex; the gap is crossed by the parabasal filament and the accessory filament. The first part of the parabasal substance is turned more or less transversely, and constitutes the beginning of the first gyre. In most species this part of the parabasal body is parallel to the next turn; it is either close to it, as in *H. riciniata* (pl. 52, figs. 42–45), or is separated by an appreciable distance, as in *H. insignita* (pl. 55, fig. 53).

The capitulum of the axostyle has undergone a striking development (pl. 54, fig. 49) in flagellates of this genus. That development is more advanced than in any other group of devescovinids except certain species of *Metadevescovina.* The membrane extended from the main body of the capitulum is prominent only in some species of *Metadevescovina,* but it is present in all species of *Hyperdevescovina.*

The main body of the capitulum (pl. 46, figs. 10, 12) is a flattened, curved structure, shaped something like a deep, incurved bowl of a spoon on the end of a stout, cylindrical handle, which is the trunk of the axostyle. The anterior part of the bowl is prolonged in a drawn-out end that lies in the region of the papilla and the place of origin of the flagella. The capitulum partly encloses the nucleus, which lies in the bowl, usually covering it on the left (cresta dorsal) and ventral sides. The dorsal prolongation of the anterior part of the capitulum into a narrow structure sometimes suggests the spathe of a jack-in-the-pulpit, the nucleus occupying the position of the projecting part of the spadix (pl. 45, fig. 3).

According to my observations, there is a membrane that comes off from the dorsal edge of the capitulum on the right side, then turns back in the manner of a completely opened door in relation to the side of the frame with its hinges (pl. 45, fig. 3). The membrane passes close to the periphery of the body. It differs in breadth and length in different species. In *H. calotermitis, H. caudata,* and *H. riciniata* (pl. 53, fig. 47) the membrane is shaped like a triangular pennant and is relatively short; in *H. falcifera* it is a wider and larger structure, but still triangular in outline (pl. 58, fig. 67); and in *H. balteata* (pl. 56, fig. 57) and *H. insignita* (pl. 54, fig. 49) it is a hoodlike, more or less quadrangular, peripheral structure that covers most of the anterior part of the body.

The position and shape of this structure correspond essentially to those of the pelta in *Pentatrichomonas hominis* (Kirby, 1945), *Trichomonas limacis* (Kozloff, 1945), *Monocercomonas verrens* (Honigberg, 1947), and certain other flagellates. It is not unlikely that this membrane of devescovinids and the pelta correspond, but since the material and preparations have not been altogether comparable, I have not here used the name "pelta" for the structure in *Hyperdevescovina.* The homology of the structures, though probable, needs to be established by further comparison.

Granules and rods occur on the capitulum and the membrane in two regions of distribution. Granules are present on the main body of the capitulum in *H. calotermitis,* where they appear to be not on the external surface but interior to the surface membrane (pl. 45, fig. 3; pl. 46, figs. 10–12). Granules in this region are not characteristic of the material that I have observed of other species, although some are present in *H. riciniata.* Rods are present on the membranous extension of the capitulum in those species where it is broad: *H. insignita, H. mitrata, H. balteata,* and *H. falcifera* (pls. 54, 57, 58). The rods are often arranged in regular patterns, are present in all specimens, and cover the whole membrane. Their appearance suggests microörganisms, but it has not been proved that they are symbiotes rather than structures of the flagellate. They are absent from species, like *H. calotermitis,* with a narrow, triangular membrane; the slender rods present at the anterior end of *H. caudata,* over the main body of the capitulum, are not related to the same membrane and possibly are on the surface.

The trunk of the axostyle is stout; it shows an internal complexity in the existence of a siderophile core around which, at least in the anterior part, are one or more inner membranes (pl. 54, fig. 49). In optical section these appear as fibrils, though I have not seen the large number that Nurse showed in illustration of the type species. If fibrils are present, they must be arranged close together in regular cylinders; the interpretation of the structure as membranous seems to be a more likely one.

*H. calotermitis* has a layer of deep-staining, close-set granules within the trunk of the axostyle in its anterior part (pl. 46, fig. 9; pl. 47, fig. 19). No similar granules have been seen in other species.

*Hyperdevescovina* is comparable to *Metadevescovina* in that the trunk of the axostyle remains stout to the end of the cytosome, and there is a projecting part that extends beyond the posterior end. None of the species of *Hyperdevescovina* that I have studied has an enlarged posterior cusp, which is often present in *Metadevescovina.* The posterior projection in *H. calotermitis* and *H. caudata* is extraordinarily long (pl. 45, fig. 1; figs. A, C), averaging about 50μ in both species and being as much as 100μ in some specimens of *H. caudata.* In certain other species, as in *H. insignita* (fig. F) and *H. balteata* (fig. G), the posterior projecting spike is only a few microns in length. The characteristic of the projecting part of the axostyle, considered, of course, only in normal specimens that have not been distorted and have not lost cytoplasm, is a feature in differentiation of species. Siderophile rings or comparable structures around the posterior part of the axostyle before it projects from the cytosome are frequently present, but marked differences occur in their characteristics in different species. Some (figs. D, F, I, J) have one or two simple rings (*H. insignita, H. mitrata, H. falcifera, H. torquata*). In *H. balteata* the structure is a cylindrical band, like a napkin ring (fig. G). *H. calotermitis, H. riciniata,* and *H. caudata* have a spiral filament. The filament may have only a few turns, and fit close to the axostyle, as in *H. calotermitis* (pl. 47, fig. 17). In *H. riciniata* and *H. caudata* there appears to be a thin membrane that bears the filament, constituting a sleeve that fits close to the axostyle anteriorly but remains cylindrical, whereas the axostyle within it tapers. The greatest development of the sleeve and the spiral filament is found in *H. caudata,* in which the sleeve is long and the spiral has many turns (pl. 50, fig. 32).

Rods similar to those that lie over the capitular membrane are present at the periphery of the cytosome, usually posterior to the middle, in most species of *Hyperdevescovina.* I have seen them in all the species that I have studied, except *H. riciniata* and *H. torquata;* and they are present in all specimens of a species. They form a belt that is just interior to the surface of the protoplasm. It is often not easy to be certain whether the rods are on the surface or in the cytoplasm. Sometimes, however, they lie more deeply, especially in the anterior part of the belt (fig. G). In the belt the rods are arranged more or less in transverse rows, with their axes longitudinal. In comparison with the rods on the surface of *Devescovina* and *Caduceia bugnioni,* those in *Hyperdevescovina* are very short and stout.

The width of the belt of rods is characteristic of a species, although considerable variation occurs. It is narrowest in *H. calotermitis,* which may have only a single row or a few transverse rows of rods (pl. 48, figs. 20, 21). In *H. caudata* the belt is also narrow (pl. 49, fig. 28). There is a broader belt in *H. balteata,* consisting of four or five transverse rows to two or three times this number (fig. G). In *H. mitrata* (pl. 51, fig. 34) and *H. insignita* (pl. 54, figs. 49, 51) rods occupy the periphery of most of the posterior part of the body.

The appearance of the rods is that of bacteria, and it is possible that they should be so identified. The studies so far made do not, however, justify a conclusion that they are microörganisms. Apparently they are of the same nature as the rods on the capitular membrane. If they are bacteria, their restriction to certain areas of the body is a notable fact in their relationship to the host.

Spirochaetes adhere to the posterior end in all species. In some they cover half or more of the body (pl. 60, figs. 72, 73); in others they are restricted to the region around the projecting axostyle (pl. 54, figs. 49, 51). Often the spirochaetes adhere only to the region of the body posterior to the belt of rods. In most instances the slender spirochaetes, which are usually 5–10μ long, are the only adherent microörganisms on this part of the body. There may, however, be some other forms also, such as the filamentous forms, 40μ or 50μ long, on *H. caudata* (pl. 50, fig. 33), and the spindle-shaped organisms on many specimens of *H. mitrata* (pl. 51, fig. 38).

Spirochaetes are adherent to the anterior end, over the capitulum, of some species (pl. 60, figs. 72, 73), but are not present on all.

### KEY TO THE SPECIES OF HYPERDEVESCOVINA

1. Length of projecting axostyle usually more than 10μ.............. 2
   Length of projecting axostyle usually less than 10μ.............. 5
2. Membrane extended from capitulum broad, rod-covered; length of axostyle projection less than 20μ.............. *H. mitrata*
   Membrane of capitulum, if present, narrow pennant-shaped; length of projecting axostyle more than 20μ.............. 3
3. Spiral filament, which surrounds trunk of axostyle before projection, with numerous turns situated on sleeve usually 5–18μ long.............. *H. caudata*
   Spiral filament with few turns, sleeve absent or shorter.............. 4
4. Gyres of parabasal body averaging 9–10, range 4–19.............. *H. calotermitis*
   Gyres of parabasal body averaging 6, range 5–7.5.............. *H. riciniata*
5. Parabasal body typically with first gyre separated from and much broader than ones following.............. 6
   Parabasal body with first gyre not markedly widened or separated from succeeding part of helix.............. 7
6. Rods of peripheral belt small, covering most of posterior part of body to near the extremity.............. *H. insignita*
   Rods of peripheral belt longer, up to 1.5μ, not extending so far posteriorly; width of belt often 8–24μ.............. *H. balteata*

**7.** **Parabasal body wound especially closely and regularly, averaging 10 turns, range 5–15; no rods over capitulum or in peripheral belt .................... *H. torquata***
**Parabasal turns less than 5; rods present over capitulum and in peripheral belt .................................................... *H. falcifera***

## COMPARISON OF SPECIES

The comparative morphology of species of *Hyperdevescovina* has been considered in the section on general morphology, and detailed comparisons between related species are made in some of the species accounts. It is desirable, however, to bring together certain information concerning differentiation of species. If my taxonomic conclusions are accepted, it is sufficient for practical purposes to ascertain the name of the host termite, and then to find the name of the one species of *Hyperdevescovina* that is found in it. For the most part, morphological differentiation of the flagellates requires well-fixed and well-stained preparations. I have based my taxonomic treatment of the group of flagellates solely upon structural characteristics. Host differences, and differences in the kind and distribution of associated microörganisms, often provide a guide to differentiation, but are not in themselves decisive.

One of the principal taxonomic characteristics that is useful in defining and differentiating species of devescovinid flagellates is the size and shape of the cresta. In *Hyperdevescovina* that characteristic is of no value, except as a mark of generic distinction; the cresta is similar in all species.

The length of the projecting end of the axostyle has a relative constancy within a population, and shows some definite differences in the flagellates of different hosts. When considered along with features of internal structure, it can be used in differentiation. A conspicuously long projection characterizes *H. calotermitis, H. caudata, H. riciniata,* and *H. mitrata.* In *H. mitrata* the length (10–23$\mu$) is usually less than the minimum, and is much less than the average of that in any of the other three species listed. In the remaining four species of the genus, the axostyle projects for a short distance that is most often less than 5$\mu$, and is normally less than 10$\mu$. (Cf. figs. A, J.)

Among the four species with a conspicuously long axostyle projection, *H. mitrata* differs also in having a wide belt of rods in the peripheral cytoplasm and a much more restricted posterior area bearing spirochaetes. (Cf. pl. 49, fig. 28; pl. 51, figs. 34, 37.) *H. riciniata* has an axostyle projection longer than that in *H. mitrata,* but much shorter than in *H. calotermitis* and *H. caudata.* The belt of peripheral rods is absent in *H. riciniata.* The anterior membrane of the capitulum is narrower, too, in that species, and rods are absent from it; in *H. mitrata* the broad rod-covered membrane is better developed than in the other three species of the group. Differences occur also among the four species in the type of ring or filament around the axostyle near the posterior end of the cytosome. *H. mitrata* has only a ring or pair of rings; the others have a spiral filament, which is shorter in *H. calotermitis* than in the other two species. (Cf. pl. 47, figs. 16, 17; pl. 50, fig. 32; pl. 51, fig. 34.)

The four species that have a very short projection of the axostyle are *H. insignita, H. balteata, H. falcifera,* and *H. torquata.* The broad first turn of the parabasal body, which extends transversely far beyond the contour of the rest of the helix, characterizes the first two species. These two species are very much alike, and differentiation has been based mainly on the morphology and distribution of the peripheral rods over the capitulum and in the belt in the posterior part of the body. The comparison is made in detail in the account of *H. balteata* (p. 354).

Besides the form of the parabasal body of *H. falcifera,* which is not notably extended in the first turn, the shape of the narrower capitular membrane differentiates that species from *H. balteata.* This difference is described in the account of *H. falcifera* (p. 357). *H. torquata* is differentiated mainly by its parabasal body, which has many gyres, the minimum number exceeding the maximum in *H. falcifera;* and the helix in the former species is closely and regularly wound from its beginning in a tapering, symmetrical figure. (Cf. pl. 59, fig. 71; pl. 58, fig. 65; pl. 55, fig. 53.)

In this section I have indicated the principal reasons for separating the species into which the genus *Hyperdevescovina* has been divided. There are other features, too, which are discussed in the species accounts. The present treatment of the genus is based, in most instances, on study of material from single host colonies. *H. caudata* was studied from a number of host colonies, and the structural characteristics were found to be relatively constant among them. Nevertheless, the present account of the genus, like those of related flagellates, must be regarded as preliminary, awaiting probable modification when fundamental studies of genetic relationships among the populations of flagellates in different groups of hosts can be made.

## MORPHOLOGY AND DIAGNOSIS OF SPECIES OF HYPERDEVESCOVINA

### **Hyperdevescovina calotermitis** (Nurse) comb. nov. emend. Kirby

(Pl. 45, figs. 1–6; pl. 46, figs. 7–12; pl. 47, figs. 13–19; pl. 48, figs. 20–24; figs. A, B)

*Caduceia calotermidis* Nurse, 1945, Trans. Roy. Soc. New Zealand, 74:306, pl. 42, figs. 1–4; text fig. 1.

*Hyperdevescovina* Kirby, 1947; type species *calotermitis* Nurse, 1945, *emend.* Kirby, 1947, J. Parasit., 33:225. (Combination *Hyperdevescovina calotermitis* not printed.)

*Type host.—Proglyptotermes brouni* (Froggatt) Emerson. New Zealand.
Banks Peninsula. (Nurse.)
T-550. Auckland. (Cleveland-Hill.) (Xenosyntype slides TP-500:248, 223, 212, 109.)

*Diagnosis.*—(After Nurse): Length 56–84μ; width 33.6–47μ; three anterior flagella; trailing flagellum a slender cord, less than body length; cresta not seen; parabasal body a single, fairly tight helix of 5–11 gyres, usually 7 or 8; capitulum of axostyle with granules; nucleus 10.7μ × 7.6μ in large forms; rod-shaped microörganisms adherent to parts of surface; spirochaetes 4–6μ long, forming a dense coat over most of surface. (Original): Length 73 (52–114)μ; width 43 (30–65)μ; trailing flagellum a slender cord about half the length of the body; cresta broad triangular with apex at blepharoplast, equal sides, posteromedial edge concave and longer than others, length 2.2 (1.7–2.8)μ; parabasal body spiraled usually 7–12 gyres, averaging 9.6, minimum 4, maximum 19, first gyre around nucleus and about twice its diameter, others turned closely around trunk of axostyle; capitulum of axostyle extended beside and anterior to nucleus in a canopy, with a long triangular membrane turned back from one margin; trunk of axostyle stout, projecting 53 (45–63)μ beyond cytosome, surrounded before projection by a spiral filament with 3–6 turns; nucleus 9 (8–10)μ × 6 (4.6–7.3)μ; granules present on inner side of longitudinal part of capitulum; spirochaetes 5–7μ long, adherent to anterior part above region of capitulum; posterior to this

**region a naked zone of variable width, followed by girdle of rods 1–2μ long lying full length just under surface; region posterior to girdle with dense coat of slightly curved rods 2–4.5μ long, adherent by one end, often interspersed with spirochaetes like those of anterior area.**

A photograph of the protozoa of *Calotermes brouni* was published by Kelsey in 1944. The flagellates that appear in it are presumably the ones here referred to as *Hyperdevescovina calotermitis.* The flagellate was described in the following year by Nurse (1945), who also reported from the same termite a species of *Oxymonas* and one of *Trichomonas.* Nurse assigned the large flagellate to the genus *Caduceia,* giving it the name *Caduceia calotermidis.* The spelling of the species name is an obvious blunder; Kirby (1947) emended it to *calotermitis,* believing that there is authority for so doing in article 19 of the International Rules of Zoölogical Nomenclature.

Nurse (1945) reported a granule, or sometimes two granules close together, at the base of the flagella. In deep-stained Heidenhain-prepared specimens the organelles seem to center in a rather large granule, which often appears irregular in shape. After further destaining, however, the anterior complex appears to be related to two smaller granules that are interconnected by a filament (pl. 45, figs. 2, 6). Each of the granules is met by one of the two roots of the flagella. The principal complex of organelles centers in the granule that is closer to the cresta. Extending posteriorly from the anterior complex, usually from the crestal granule, but sometimes apparently from the other one, is an elongated, often curved mass of similarly staining substance, which is not smoothly outlined and is variable in size (pl. 45, figs. 4, 5). Extending ventrally from the granule farthest from the cresta is an uneven band of stainable material that passes to the edge of the capitulum and is probably part of the structure of the capitulum (pl. 45, figs. 2, 4, 6).

The nuclear rhizoplast is distinct in some preparations. It extends from the anterior granule complex to the nearest part of the nuclear membrane, then turns and extends along the surface of the nucleus for a short distance (pl. 45, fig. 4; pl. 46, fig. 8). Except for its slender anterior part, the nuclear rhizoplast is band-formed; in some specimens the band is broader than in others.

The accessory filament is a conspicuous structure, which is stained black in preparations when the parabasal filament, even in the spiral part of the parabasal body, is not visible. The shape and the position of this structure are constant. It leaves the granule nearest to the cresta as a filament and proceeds close to the anteromedial edge of the cresta (pl. 45, fig. 6; pl. 46, fig. 7). After continuing, slightly curved toward the nucleus, it bends sharply dorsally, almost in the manner of a sickle from the handle, then turns abruptly inward again and extends transversely along the first part of the spiral of the parabasal body. Beyond its first bend it broadens abruptly to a band, which is broader in some specimens (pl. 45, fig. 4; pl. 46, fig. 8) than in others. This broadened distal part of the accessory filament is a striking structure, which differs from the entirely filamentous structure in a corresponding position in *Hyperdevescovina caudata.* Because in *H. calotermitis* the terminal part of fig. 9). The nuclear axis bends sharply toward the right and dorsally from the point at which this part of the axostyle meets it (pl. 46, fig. 12; pl. 47, figs. 14, 19). On the ventral side the outermost sheath of the axostyle is separated from the inner structures by a space of only moderate width, and continues forward as the membrane of the capitulum. On the dorsal side the outermost sheath extends a much greater distance from the core, meeting the nucleus near or anterior to the middle of its length, and continuing into the capitulum (pl. 46, fig. 12). Between the sheath and the core, on the dorsal side, is thus delimited an area that in optical section is subtriangular. This area is crossed by a band that extends from the outer membrane of the core parallel to the outermost sheath (pl. 46, fig. 12). In some preparations the band appears brownish, like the parabasal body, instead of black, like the axostyle sheaths. The band may be an optical section of another tubular membrane.

In the majority of specimens there are small granules within the trunk of the axostyle in the region of the anterior expansion (pl. 45, fig. 1; pl. 46, figs. 8, 10). The number of granules varies, and sometimes there are none. They are never present in the inner core and do not extend peripherally as far as the outermost sheath. The presence of small granules is particularly characteristic of the dorsal area, in which the sheath extends widely away from the core; in that region the aggregation is dense. Granules extend from this mass forward alongside the nucleus, and in a thinner layer usually only one granule thick on the left and ventral sides in the trunk of the axostyle (pl. 47, fig. 19). There is an area on the right side of the axostyle that is always free of granules. The granules stain deeply with both iron-haematoxylin and Delafield's haematoxylin after fixation in Schaudinn's fluid.

Around the trunk of the axostyle, just before its projection from the cytoplasm, is a close-fitting, apparently spiral filament usually of three or four but sometimes more turns (pl. 47, figs. 16–18). It is not a simple matter to ascertain whether there is a single continuous filament or a series of rings, but the interpretation of a spiral filament seems to be the more likely one.

The substance of the axostyle is continued forward as the capitulum, the base of which constitutes a cup-shaped structure in which the posterior end of the nucleus is set. On the left side and part of the ventral side, the capitulum extends far forward and transversely across the anterior part of the body, forming a sort of canopy over the nucleus (pl. 45, fig. 3; pl. 46, fig. 12). Where it passes forward, the capitulum extends almost halfway around the nucleus, leaving the right side and part of the ventral side open. In its middle part the capitulum bulges far to the left side, away from the nucleus, the axis of which slants toward the right (pl. 47, figs. 14, 19). Near the level of the anterior end of the nucleus, the membrane passes transversely, continuing beyond the point of contact with the anterior granule-complex in a narrowing membrane that ends as a filament (pl. 47, fig. 7). The ventral edge of the capitulum, for a distance of 3 or 4$\mu$ beginning shortly after it leaves the trunk of the axostyle, is extended in a long, triangular membrane (pl. 45, fig. 3; pl. 46, fig. 10). The membrane turns back from the ventral edge, somewhat as a wide-open gate swings back from the wall from which it is suspended, although the angle is not a sharp one. The triangular membrane extends transversely, curved parallel to the main part of the capitulum, and situated not far from the periphery of the body. Outwardly it is concave. The foregoing description of the shape of the capitulum is somewhat oversimplified; various irregularities and folds in the membranes give it a very complex character.

The longitudinal part of the capitulum is beset with numerous rounded granules, which apparently are always present, though they vary in number (pl. 45, figs. 2–3; pl. 46, figs. 8–11). They are similar in size and shape to those in the conical area in the core of the trunk. They are much larger in size than the abundant granules in the outer part of the trunk of the axostyle of many specimens. The capitular granules stain well with iron-haematoxylin; but they are faintly stained in Delafield material in which the parabasal body, the chromatin, and the small granules of the trunk are stained intensely. They are not situated on the exterior surface of the capitulum, but, as is apparent in optical section, are immediately interior to the surface membrane (pl. 45, fig. 3). This membrane appears to be appreciably thinner than the external sheath of the trunk of the axostyle. The granules are possibly embedded in the substance of the capitulum; but my observations are not in disagreement with the possibility that they are applied to its inner surface in a single layer.

Nurse showed many longitudinal lines in the trunk of the axostyle posterior to the nucleus (his pl. 42, figs. 3, 4), giving it the appearance of being fibrillar. So far as my observations have shown, his representation is an exaggeration of the number of lines that in optical section appear to be present.

Except for its first gyre, the parabasal body is usually turned in a rather tight, close helix around the anterior part of the trunk of the axostyle (pl. 46, fig. 11). Because this part of the axostyle narrows posteriorad, the parabasal spiral is narrower in its posterior part, where usually it has no more than two-thirds of its anterior diameter. The first gyre is turned around the capitulum and the nucleus. It is close to the rest of the helix in both its proximal and its distal parts, but its middle part is more or less drawn away from the next gyre; the gap is sometimes as wide as three or four of the spiral turns. The first gyre extends at a distance away from the left side of the nucleus, where it must extend around the capitular membrane (pl. 47, fig. 14). In this region the parabasal body is related to the triangular flap of the capitulum. This triangular membrane is concave outwardly, and constitutes a trough in which, for part of its length, the parabasal body fits; but the parabasal body is near the posterior edge, not in the middle, of the trough (pl. 45, fig. 3). Two specimens have been found in which the parabasal body was wound tightly in many turns around the trunk of the axostyle for nearly the entire length of the cytosome (pl. 47, fig. 15).

The thickness of the parabasal body is the same for all its length, and it is rounded without tapering at both the posterior and anterior ends. The anterior end of the Delafield-staining substance is at a distance of several microns from the anterior granule-complex (pl. 47, fig. 13). The gap presumably is crossed by a delicate parabasal filament, but ordinarily the only structure that can be seen in that position is the accessory filament. The parabasal thread on the inner edge of the helix (pl. 46, fig. 7) is a filament or narrow band, which in certain preparations fades out anteriorly and posteriorly. Sometimes the parabasal substance shows small vacuoles varying in size and position (pl. 47, fig. 13).

Most specimens contain an abundance of wood, usually in particles of relatively small or moderate size (pl. 45, fig. 1), but occasionally relatively large pieces, which may be as long as the body. The distribution of wood is not restricted to any particular region of the cytosome; but the most anterior part alongside the capitulum is not occupied, and a variable zone of the peripheral cytoplasm is free. The region occupied by wood may extend almost to the periphery; or it may be confined, at the other extreme, to half or less of the width of the body (pl. 48, fig. 23). There is no structurally differentiated cortical zone of cytoplasm; the area left free of wood, whatever its extent, has microscopically the same apparent cytoplasmic structure as the rest.

Present also in many specimens, and abundant in a few, are spherules of variable size that stain with iron-haematoxylin and show a vacuolated interior (pl. 48, fig. 22). These are probably not ingested as such; possibly they are products of metabolic activity. Their presence is, however, not sufficiently constant to warrant the supposition that they are regularly formed in the course of digestion and assimilation.

Straight or curved rods, 1–4$\mu$ long, are constantly present among the wood particles (pl. 48, figs. 23, 24). They are abundant, and show a significant distributional relationship to wood. When the wood is aggregated in the central part of the cytosome, the rods are also restricted to that region; wood particles and rods are always interspersed in the same area.

The surface of the body over the expansion of the capitulum of the axostyle, where this comes close to the surface, is covered with a dense coat of spirochaetes 5–7$\mu$ long (pl. 48, fig. 21). The correspondence between the capitulum and the area of distribution of these organisms is rather close, but it is not complete.

Posterior to this group of spirochaetes is a zone of variable breadth and shape that is devoid of microörganisms (pl. 48, fig. 20). The body surface posterior to that zone, a region that usually amounts to from a quarter to a half of the length of the flagellate, is always densely covered with microorganisms (pl. 48, fig. 20). This surface covering is sometimes symmetrically disposed around the posterior part of the body; often there is more of it on one side than on the other; and in some instances it is restricted almost entirely to one side (pl. 48, fig. 21). In the last instance, the edge of the area on one side may come very close to, or even establish contact with, the anterior group of spirochaetes.

At the anterior margin of this posterior, microörganism-covered region is a band of short rods (fig. B; pl. 48, figs. 20–21) that are rounded at their ends, and lie parallel to the body surface. The arrangement that might be considered typical is a band of a single row of regularly spaced, parallel rods encircling the body; but this ideal arrangement is seldom realized. Various irregularities modify the parallel position (fig. B). The spacing is variable, and in places the band is sometimes two or three rows broad, though most often there is a single row. The rods lie at or near the surface, and it is difficult to ascertain whether or not they are exterior. It is probable that they are actually in the cytoplasm, but are in contact with the surface layer.

The region posterior to the rods bears a dense coat of two kinds of microorganisms. Rods, somewhat more slender than those just described but two or three times as long, slightly curved, and adherent by one end, are present in abundance on the entire area (pl. 45, fig. 1). Often interspersed with them are spirochaetes like those of the anterior area (pl. 48, fig. 21); but frequently spirochaetes are lacking from certain parts of the rod-covered surface, especially near the posterior end. No long spirochaetes are present like those on the posterior region of *H. insignita* and *H. caudata*.

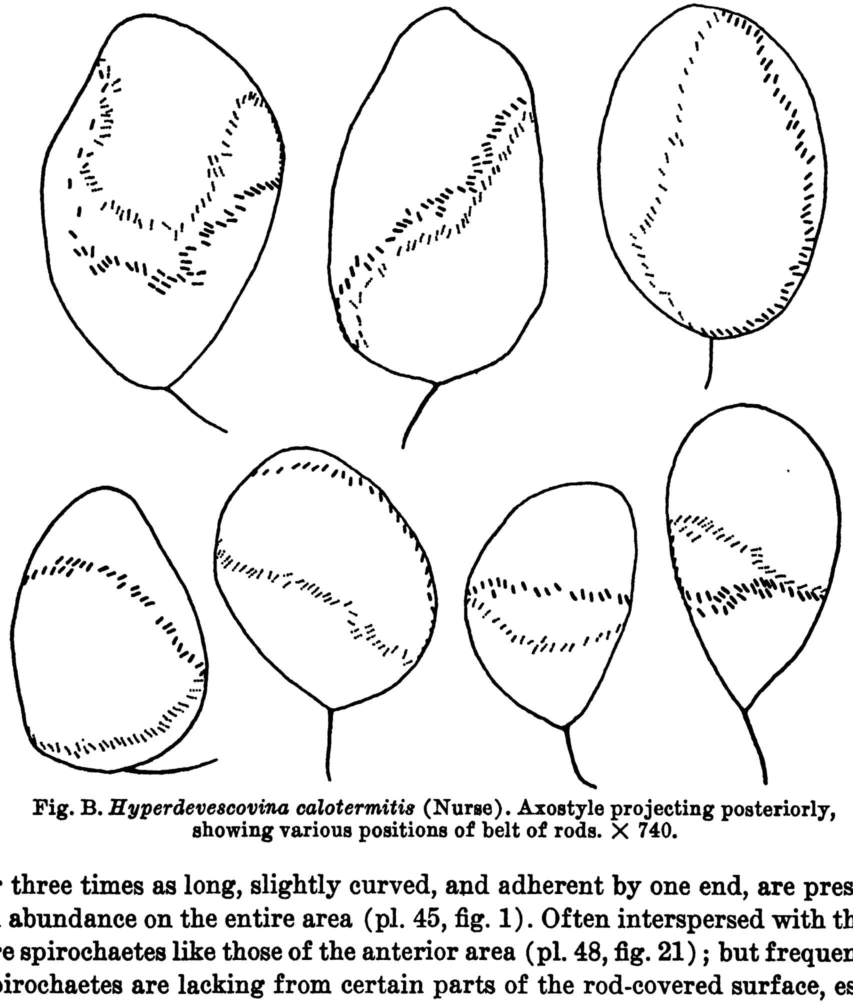

Fig. B. *Hyperdevescovina calotermitis* (Nurse). Axostyle projecting posteriorly, showing various positions of belt of rods. × 740.

Nurse brought about disappearance of the spiral bacteria from the flagellate by feeding the termites for a month on filter paper soaked in 5 per cent acid fuchsin. After this treatment the rod-shaped organisms attached to the surface were still present. They were observed to detach themselves and to become attached again. Nurse called attention to the striking difference in activity between the flagellates bearing spirochaetes and those from which spirochaetes had been removed. The former flagellates swam smoothly and vigorously, whereas the spirochaete-free ones were almost immobile. This observation led Nurse to suggest that the spirochaetes play a part in the locomotion of the flagellate. It is inconceivable that the activity of adherent microörganisms should be so coördinated that they are able to function in the manner of cilia in the locomotion of their host. It is apparent from Nurse's account of the sending out of cytoplasmic protrusions, and his description of the turning of the parabasal body and the axostyle with the mobile anterior region, that the spirochaete-free flagellates from the fuchsin-fed termites were not in a normal condition.

### **Hyperdevescovina caudata** sp. nov.

(Pl. 49, figs. 25–28; pl. 50, figs. 29–33; fig. C)

*Type host.*—*Proglyptotermes* sp. nov. South Africa.
T-4072. Near King William's Town, Cape Province. (Syntype slides TP-2095:7, 3, 1.)
T-4043. Near Port Shepstone, Natal. (Xenosyntype slides TP-2085:7, 14, 23.)
T-4051. Near Flagstaff, Natal. (Xenosyntype slide TP-2090:13.)

*Diagnosis.*—Length 78 (37–139)μ; width 50 (24–78)μ; trailing flagellum a slender cord 50–70μ long; cresta broad triangular with apex at blepharoplast, equal sides, posterior edge more or less deeply excavated, length less than 2μ; parabasal body turned in close spiral around nucleus and axostyle 6–17 turns, averaging 9.2 turns, anterior part almost transverse in a loop that usually is not notably wider than next posterior gyre; capitulum of axostyle expanded beside and anterior to nucleus and continued in a narrowing membrane around nucleus; trunk of axostyle in average-sized specimens 6–7μ wide immediately posterior to nucleus, decreasing rapidly to about 3.5μ, then tapering gradually to about 2μ at posterior end of cytosome; axostyle differentiated into a sheath surrounding other tubular elements and a central strand; axostyle continued posteriorly in long tapering projection extending 22–106μ, averaging 53μ, beyond cytoplasm; trunk of axostyle before projection from body surrounded by a sleeve often 5–18μ long, bearing a spiral filament with numerous close turns; nucleus 9 (4.5–11.5)μ × 5.4 (4.5–7)μ; slender rods present at periphery of body over capitulum, slender rods at periphery of body in belt usually near middle, several rows broad; slender, short spirochaetes adherent in dense group at anterior end over capitulum, and to whole part of body posterior to belt of rods; stout, longer spirochaetes, many 40–50μ long, present in numbers adhering to surface of body posterior to belt.

As observed in living material, the body is oval or pyriform in shape, and is notable for the fact that the axostyle projects free beyond the posterior end for a length that frequently equals or exceeds that of the body. There is a well-marked anterolateral papillary projection, at the end of which the three anterior flagella become free.

The apical point of the cresta is close to the anterior granule-complex. The granule, at the place where most anterior structures meet, appears to have the shape of a comma, being prolonged posteriorly as a short rod (pl. 50, fig. 31). Originating from the anterior part of the granule and passing along the external edge of the cresta is the trailing flagellum, which is slender in its proximal part (pl. 50, fig. 31). In its anterior part the same granule gives rise to a flagellar root that eventually divides into two anterior flagella. The third flagellum ends near this granule in an angular enlargement that is connected to the granule by a short filament (pl. 50, fig. 31). From the anterior granule-complex the nuclear rhizoplast passes in a transverse or oblique direction to the anterior surface of the nuclear membrane (pl. 50, fig. 29).

The accessory filament originates from the granule to which the cresta is related as a slender filament that passes along the anteromedial edge of the cresta (pl. 49, fig. 25; pl. 50, fig. 31). Near the posterior end of the cresta the filament undergoes a bend, which is usually sigmoid in form; at the same place the structure becomes much stouter than before. In its distal part the accessory filament extends transversely parallel to the first gyre of the parabasal body, between this and the second gyre. It lies close to the parabasal body, but at least in many specimens it seems not to be in actual contact with it. After paralleling the parabasal body for a short distance, it ends abruptly.

On the anterior side of the accessory filament is the slender parabasal filament (pl. 50, figs. 29, 30). This extends in a smooth curve, and does not follow the accessory filament in the sigmoid bend which that structure often has.

The anterior end of the Delafield-staining substance of the parabasal body is close to the nuclear membrane at some distance from the anterior granule complex (pl. 49, fig. 25). This gap is crossed by the parabasal filament. Within the parabasal helix, the filament lies at the inner edge of the substance of the parabasal body. It is band-formed and occupies the full breadth of that inner edge, and it stains more deeply than the other parabasal substance with iron-haematoxylin (pl. 50, figs. 29, 30). In Schaudinn-Delafield preparations the parabasal substance appears to contain numerous small vacuoles of variable size and irregular distribution (pl. 49, fig. 27).

The trunk of the axostyle is similar to that of *Hyperdevescovina calotermitis,* and there is a similar long, pointed projection (fig. C; pl. 49, fig. 25). Surrounding the axostyle near the posterior end of the cytosome is a sleeve of variable length (pl. 50, fig. 32). In a number of specimens the length of the sleeve ranged from 5 to 18$\mu$. At its anterior end the sleeve is closely applied to the axostyle, whereas at the posterior end, where the diameter is somewhat greater, it is more or less separated from the axostyle. The sleeve bears a closely wound spiral filament (pl. 50, fig. 32).

In the expanded anterior part of the trunk of the axostyle, the apparent fibrillar structure is especially evident. This may be regarded as at least in part an appearance based on optical sections of membranes; but it is not easy so to account for the twisted fibrillar appearance of the axostyle represented by plate 50, figure 30. In the region within the parabasal helix, five apparent fibrils are often visible on each side of the axostylar core (pl. 50, fig. 30). These necessarily approach one another in the narrower part of the axostyle, and are then not separately distinguishable. In the greater part of the trunk of the axostyle only one or two membranes, aside from the outer sheath, can be seen surrounding the core. Within the core is a central filament (pl. 50, fig. 32).

The capitulum of the axostyle is in general similar to that of *H. calotermitis,* but it is not so large; and the flaplike, subtriangular membrane is not so conspicuously developed. Granules are absent both from the trunk of the axostyle and from the capitulum of *H. caudata.*

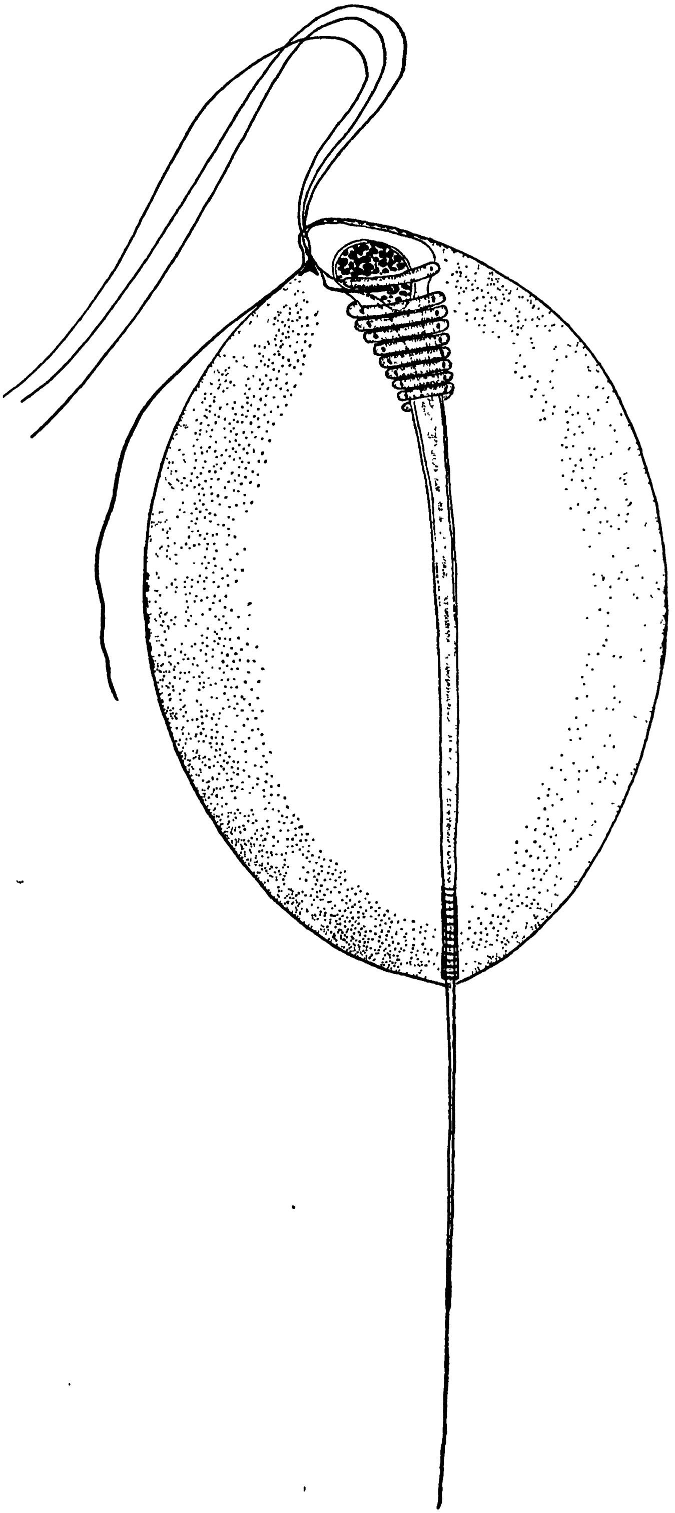

Fig. C. *Hyperdevescovina caudata* sp. nov. from *Proglyptotermes* sp. nov. South Africa. Adherent spirochaetes omitted. Peripheral rodlets anterior to capitulum and in belt around body are shown only at edges. × 1500.

The longer diameter of the nucleus is oblique in position relative to the longitudinal axis of the body, and the outline of the nucleus is somewhat irregular (pl. 50, fig. 30). In the preparations studied, a fairly broad, clear zone was sometimes present between the membrane and the chromatin mass, but usually this space is narrow or absent. A single, spherical, relatively rather large nucleolus is usually present. It sometimes showed a composition of several granules in a matrix substance. Occasionally, several deep-stained nucleolar bodies are present in the chromatin mass (pl. 50, fig. 31).

At the anterior end of the body are numerous short, slender rods parallel to the surface (pl. 49, fig. 26). The area occupied by the rods corresponds to the whole anterior surface of the capitulum. They are not on the capitular membrane, however, but at the periphery of the cytoplasm (pl. 50, fig. 29). It is often difficult to be sure whether they are exterior, adherent to the surface, or whether they are in the cytoplasm; but it seems most probable that they are just anterior to the pellicular membrane. A frequent length of the rods is about 1$\mu$, but they vary. They are often arranged in a more or less orderly manner in parallel, curved rows, the rods in each row being placed like the ties of a railroad track. There are, however, various irregularities in their position.

Adherent to the same region of the anterior end is a dense group of slender spirochaetes, many of which are about 4$\mu$ long (pl. 50, fig. 33). Except for these rods and spirochaetes, which are restricted to a small area, the surface of the anterior part of the body is without adherent microörganisms. The posterior part, including more or less than half of the body, is densely clothed with short, slender spirochaetes like those on the anterior end (pl. 50, fig. 33; pl. 49, fig. 28). Besides these, on the same region, are numerous long, stout, filamentous microörganisms, many of which are about 40$\mu$ long and some of which exceed 50$\mu$. These long filaments are usually absent from the anterior part of the devescovinids, but sometimes a few are present on the anterior end.

Immediately anterior to the posterior coat of spirochaetes is a belt (pl. 49, fig. 28) of the same kind of rods that are present in the region of the capitulum. The rods are more or less parallel to one another in a longitudinal direction, arranged in rows. The belt is two, three, or more rows wide. In some specimens single rows are continuous around a large part if not all of the body. More frequently, however, rows are interrupted, each running in an oblique direction and stopping when the coat of spirochaetes is reached. In relation to the surface layer of the body, the position of these rods is like that of the rods over the capitulum; they lie just interior to the pellicular layer of the cytoplasm.

Posterior to the parabasal body, the cytoplasm usually contains many particles of wood. Present also are numerous large granules that are stained by iron-haematoxylin.

*Hyperdevescovina caudata* and *H. calotermitis* have the same size and shape, and the same sort of long projecting axostyle, resembling each other closely. They occur in termites that are widely separated geographically, one occurring in New Zealand and the other in South Africa. Differences exist in the type of adherent microörganisms, but in internal structure the differences are only in small points. It would be difficult, aside from the guide provided by the difference in hosts and in adherent microörganisms, to distinguish the two flagellates except in well-stained preparations. In a comparison of specimens set up side by side on two microscopes, I have noted the following points of difference:

In *H. calotermitis* the capitulum of the axostyle is relatively larger; to accommodate it there is more space between the anterior end of the nucleus and the anterior end of the body. The dorsal domelike development of the capitulum of the New Zealand species is more marked.

The conspicuous triangular membrane that appears as though turned back from an edge of the capitulum near the nucleus in *H. calotermitis* does not appear in the same manner in *H. caudata.*

The slender rods at the surface of the body over the capitulum of *H. caudata* are not present in *H. calotermitis,* and the granules present in the rounded part of the capitulum of *H. calotermitis* are not present in the other species.

A definite difference is found in the accessory filament. In *H. caudata* that structure is a filament for all its length, though it is especially stout in its distal part. In *H. calotermitis* the accessory filament bends more sharply where it comes in contact with the parabasal body, and in this part it is broadened, sometimes to a rather broad band. Moreover, it comes in closer contact with the first gyre of the parabasal body than does the accessory filament of *H. caudata.*

The small, deep-staining granules that are present in the trunk of the axostyle, just posterior to the nucleus, in *H. calotermitis* were not seen in *H. caudata.*

In the preparations that I have studied, *H. calotermitis* did not have the sleeve with a closely wound spiral filament of many turns that surrounds the posterior part of the trunk of the axostyle in the cytosome of *H. caudata.* Instead, the New Zealand flagellate had a spiral filament of only a few turns.

### **Hyperdevescovina mitrata** sp. nov.

(Pl. 51, figs. 34–38; pl. 52, figs. 39–40; fig. D)

*Type host.*—***Proglyptotermes pallidinotum*** (Hill) Emerson. Australia.

T-517. (Hill 3236.) New South Wales, Pigeon House Range. (Syntype slides TP-517:12, 16, 22.)

*Additional host.*—***Proglyptotermes tillyardi*** (Hill) Emerson. Australia.

T-325. (Hill.) Aust. Cap. Terr. (Homosyntype slides TP-304:5, 14.)

T-504. (Cleveland-Hill.) Canberra. (Homosyntype slides TP-504:1, 5.)

*Diagnosis.*—(From type host): Length 54 (40–70)μ; width 35 (24–47)μ; anterior flagella 40–50μ long; trailing flagellum a cord, shorter than body; cresta 2–3μ long, equal sides; parabasal body in close helix of 4–6 gyres, first gyre somewhat broader than pattern of the others; capitulum of axostyle extended in broad caplike membrane over anterior part of body, rods arranged over outer surface of this membrane; trunk of axostyle stout within body, with slender posterior projection 10–23μ long; nucleus 8.4 (7.3–9.3)μ × 4.7 (4.0–5.3)μ; broad belt of peripheral rods around most of posterior part of body; slender spirochaetes adherent to surface of body posterior to belt of peripheral rods; spindle-shaped organisms, often 3–7μ long, with free end drawn out in a filament adherent to surface among spirochaetes. (From *P. tillyardi* T-504): Length 55 (48–61)μ; width 37 (30–45)μ; anterior flagella 60–70μ long; cresta 2–3μ long; parabasal gyres 4.5–7; projection of axostyle 8–15μ long; nucleus 9.6 (8–11)μ × 6.3 (5.5–7)μ. (From *P. tillyardi* T-325): Length 46 (33–61)μ; width 30 (19–41)μ; cresta 1.5–2.5μ long; nucleus 7.5 (6–9.3)μ × 5.1 (4–6)μ.

Hill (1942) stated that *Calotermes pallidinotum,* which he described in that paper as a new species, is closely allied to *C. tillyardi* Hill, 1932. The existence of the same species of *Hyperdevescovina* in the two termites is significant in its bearing on the relationship of the hosts.

As is usual in devescovinids of this group, the three anterior flagella have two roots that end separately. At the proximal end of the root nearest to the cresta a small granule often appears, immediately posterior to which is a larger body of irregular shape (pl. 51, fig. 36). The other root of the anterior flagella ends separately a short distance away. Arising from the first granule, the nuclear rhizoplast passes posteriorly along one side of the irregular body, and the parabasal filament passes along the other side. The nuclear rhizoplast is a stout filament that passes to the nuclear membrane and runs for a short distance along its surface. In some specimens it appears to be broadened to a band in the region where it meets the nucleus, but the band form is much less developed than in *H. calotermitis.*

In preparations of this species it was possible to observe separately the anterior parts of both the parabasal filament and the accessory filament. The proximal part of the accessory filament is very slender and lies close to the anteromedial edge of the cresta. Posterior to the cresta the structure is moderately stout. It extends for a short distance longitudinally, then turns transversely, broadens to a band, and comes into contact with the posterior edge of the first turn of the parabasal body. The parabasal filament is a well-defined and rather heavy fibril, though not so stout as the distal longitudinal part of the accessory filament. It parallels the accessory filament in both the transverse and the longitudinal parts. Between the two filaments a clear space appears in suitably oriented specimens.

The parabasal body is characterized by a notable broadening of the first gyre in relation to the following parts of the helix (pl. 51, fig. 34). The size of the gyre is correlated with a marked protuberance ventrally of the capitulum of the axostyle, and a deep concavity of the capitulum anterior to the protuberance. The parabasal body passes close around the posterior border of this concavity.

The axostyle is extended in a broad, peripheral, caplike membrane over the anterior part of the body. The membrane is similar in shape to that of *H. insignita;* it is shown more completely in the drawings of that species than in those of *H. mitrata.* The whole of the membrane is marked by rods that lie exterior to it, arranged more or less in rows (pl. 51, fig. 35; pl. 52, figs. 39, 40). The rods lie close to the inner side of the surface of the body, but their relationship is to the capitular membrane. The body may be distorted so that the membrane lies deep in the cytoplasm; the rods are then still in their usual position in relation to it.

In the region of the posterior part of the parabasal helix, the trunk of the axostyle has a diameter of about 3μ. It gradually decreases in diameter until it measures about 1.5μ near the end of the cytosome. It then undergoes a rapid decrease in diameter, becoming a filament, which projects posteriorly from the body (pl. 51, fig. 34; fig. D). The length of the projection is moderate; it is much shorter than in *H. caudata,* but longer than in several other species.

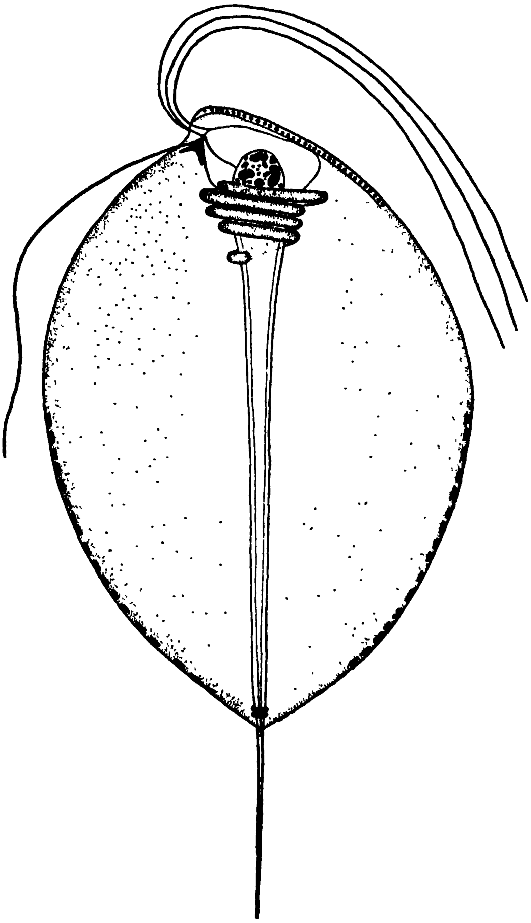

Fig. D. *Hyperdevescovina mitrata* sp. nov. from *Proglyptotermes pallidinotum.* Australia. Adherent spirochaetes omitted. Peripheral rods of broad belt around posterior part of body are shown only at edges. × 1500.

On certain iron-haematoxylin–stained slides that were examined, the filamentous terminal part of the axostyle was black, whereas the stouter part within the cytosome was gray. Surrounding the region just posterior to the place of rapid decrease in diameter are two or three rings (fig. D), or possibly a short spiral filament. The length of the region occupied by the iron-haematoxylin–staining element is 2–3μ. Some specimens have a projection of part of the stout trunk of the axostyle. In such specimens it may be seen that a minimal amount of cytoplasm covers the axostyle to the place, just posterior to the rings, where the true projection spike begins.

There is a wide belt of rods around the posterior part of the body, covering an area from near the middle of the body or more anteriorly to a point not far from the posterior end (pl. 51, fig. 34). The rods are peripheral in position, but within the cytoplasm; they may lie rather deeply in some distorted specimens.

Posterior to this belt of rods, spirochaetes are adherent to the surface of all specimens (pl. 51, fig. 37). On many specimens, microörganisms of another kind are adherent among the spirochaetes. The number of these varies; usually they are not abundant. They are straight or curved bodies; many are 3–7$\mu$ long. Some, presumably not fully developed, are comparatively slender. Most of them are stout in the middle part and have a spindle shape. One end is pointed and attached to the surface of the body; the other end is drawn out into a filamentous prolongation (pl. 51, fig. 38).

In about half of the specimens of *H. mitrata* from one of the two colonies of *Proglyptotermes tillyardi,* the cytoplasm contained deep-staining rods 1–3$\mu$ long (pl. 52, figs. 39–40). The main grouping of those rods is alongside of and anterior to the nucleus. When they are restricted to one side of the nucleus, it is always the right side. They are arranged in a single layer and are oriented in various directions. They lie against the adnuclear part of the capitulum and in the space between it and the capitular extension. In most specimens in which these rods are present on the capitulum, similar rods are distributed in the general cytoplasm. The rods in the posterior cytoplasm have not been found in the absence of the rods near the nucleus. In the cytoplasm each is surrounded by a narrow, clear zone.

I made some observations on living *H. mitrata* from *Proglyptotermes tillyardi* that had been collected at Corse Creek, Australian Capital Territory, and sent to me by G. F. Hill.

The rods of the anterior part of the body were observed in the living material to be almost always present in abundance. In places they appeared at a distance interior to the surface, and the layer of them extended only about halfway around the body. The membrane of the expanded capitulum was not noted as such in the living specimens, but it was observed that the relationship of the rods was apparently to this structure.

Spirochaetes were abundant on a variable part of the body, often amounting to half or less, sometimes more. The anterior part of the body, which appeared clearer than the rest because wood particles were usually not present, had few spirochaetes or none. The type of movement and the irregularity in distribution of the filaments showed clearly that they were spiral microörganisms.

Rotation of parts of the body, independently of one another, was observed in many specimens examined in salt solution on slides. In one specimen the anterior two-thirds of the body was wedged in a mass of debris, and the posterior part of the body was rotating rapidly and continuously in a clockwise direction as viewed from a posterior position. This continuous rotation involved only the posterior three-fourths of the body, most of which had a coat of spirochaetes that were in very active vibration. The anterior part of the body occasionally turned with the rest, but often it either turned at a slower and more irregular rate or remained fixed in one position. When the posterior part was revolving rapidly, and the anterior part, along with the mastigont structures including the axostyle and parabasal body, was stationary, there must have been much turmoil in the cytoplasm of the region near the posterior part of the parabasal body. Similar rotational movements were observed in other animals not embedded in debris.

Other specimens were watched in which the posterior part of the body remained fixed, whereas the anterior part, together with parabasal body, axostyle, and all the anterior cytoplasm, including the surface, turned irregularly in a counterclockwise direction as viewed from the rear. This sort of rotation is common in these flagellates confined under a cover glass in salt solution. Sometimes only occasional, partial turns of the anterior part take place; at other times, rotation is continuous, though somewhat irregular.

In many of the flagellates, rotation involving the whole body may be seen. That should be the normal occurrence when there is no pressure on, or confinement of, part of the body.

### **Hyperdevescovina riciniata** sp. nov.

(Pl. 52, figs. 41–45; pl. 53, figs. 46–48; fig. E)

*Type host.*—*Proglyptotermes atratus* (Hill) Emerson. Australia.
T-505. (Hill-Cleveland.) Aust. Cap. Terr. (Syntype slides TP-505:11, 13, 20.)

*Diagnosis.*—Length 63 (44–78)μ; width 33 (24–47)μ; anterior flagella 40–55μ long; trailing flagellum a slender cord 50–60μ long; cresta broad triangular with apex at blepharoplast, excavated posteriorly, length 2–3μ; parabasal body turned in compact, funnel-shaped helix of 6 (3–7.5) gyres, anterior gyre not separated from, or notably wider than, that posterior to it, all turns around trunk of axostyle; capitulum of axostyle shaped like that of *H. calotermitis,* membrane covering mostly left and ventral sides of nucleus, with long triangular membrane turned back from right margin; trunk of axostyle projecting 30–42μ from posterior end of body in pointed spike, before projection surrounded by a sleeve 4–5μ long, bearing a chromophile spiral filament; nucleus 6.9 (6–8)μ × 4 (3.3–4.7)μ; no rods present over capitulum or in peripheral belt around body; spirochaetes, many 5–7μ long, adherent to capitular region and posterior half or two-thirds of body.

The structures of the mastigont meet anteriorly in a complex of interconnected granules. Close to the end of the cresta is a granule-like enlargement; this gives rise anteriorly to a curved rod that extends in a direction parallel to the external edge of the cresta (pl. 53, fig. 47). The anterior flagella meet the complex in two rather widely separated roots. The root nearest the cresta consists of the proximal parts of two anterior flagella; it ends in an enlargement that is close to the first granule. Posterior to the enlargement is an appendage (pl. 53, fig. 47) like that characteristic of many larger devescovinids; it is variable in size, elongated in shape, and sometimes appears like a granule borne on a stalk. The parabasal filament passes along the dorsal side of this appendage and the nuclear rhizoplast along the ventral side. Connected to the enlargement which these structures meet is a granule that is met by the root of the third anterior flagellum. This enlargement continues ventrally in a fibril that appears to belong to the capitulum of the axostyle.

Passing posteriorly from the granule nearest the cresta, which gives off the curved rod anteriorly, is the accessory filament (fig. E). In its first part this

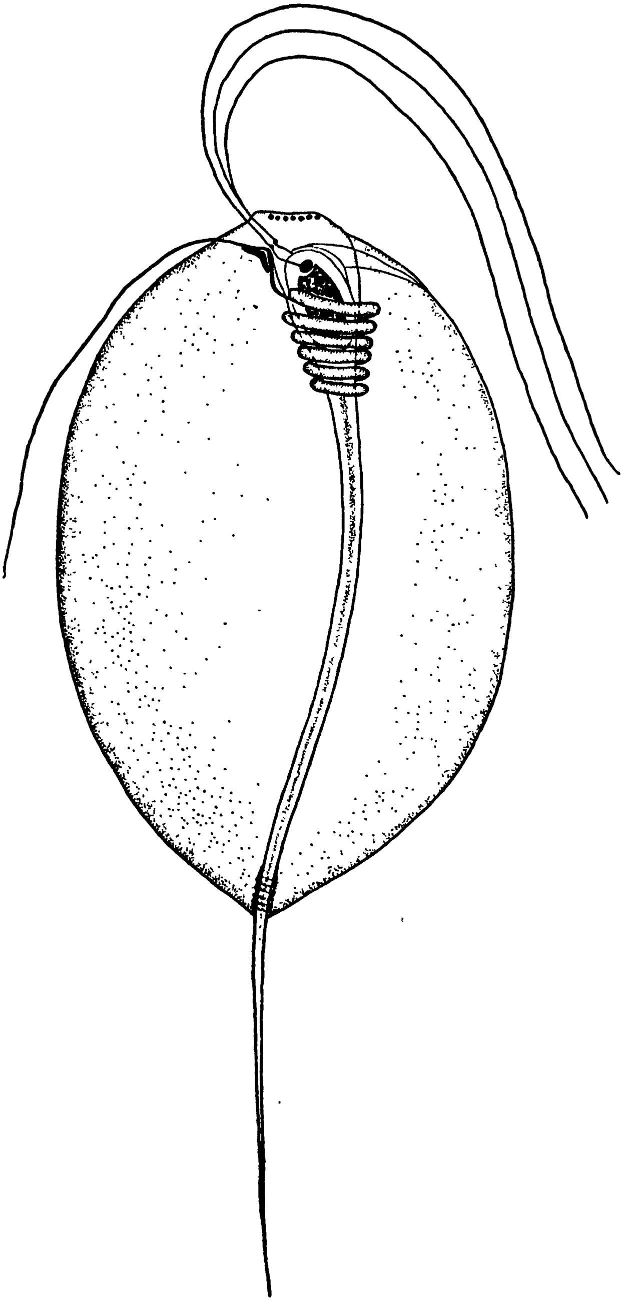

Fig. E. *Hyperdevescovina riciniata* sp. nov. from *Proglyptotermes atratus.* Australia. Adherent spirochaetes omitted. × 1500.

filament is close to the anteromedial edge of the cresta. In its course it has an elbow-like bend similar to that of *Hyperdevescovina calotermitis.* In the region of the bend and distally it is broadened to a band. The distal part of the accessory filament is parallel and close to the posterior edge of the first transverse part of the parabasal body.

The nuclear rhizoplast is a stout filament that meets the nuclear membrane, then turns and runs for a short distance along its surface.

Successive turns of the parabasal body are close together and are wound closely around the axostyle (pl. 52, figs. 42–45). The first turn is not especially separated from, or wider than, the one posterior to it, as it is in *H. insignita* and some other species. The anterior end of the main substance of the parabasal body is not far separated from the adjacent gyre, and is at some distance from the anterior complex of granules. The parabasal filament and accessory filament thus cross a rather wide gap. Some specimens have a short ramus of the parabasal body that arises in a variable position from the anterior to the posterior part and is directed between two turns of the main substance (pl. 52, figs. 43–45).

The capitulum of the axostyle (pl. 52, fig. 41; pl. 53, fig. 47) is shaped much like that of *H. calotermitis.* Its form is that of a deep ladle, extending to a point at its end, with the nucleus fitted into the bowl near the handle, which is the trunk of the axostyle. The nucleus does not lie flat in the bowl, but extends obliquely upward from it. The capitular membrane covers mostly the left and ventral sides of the nucleus; the apical part of the bowl is anterior to the nucleus. From the right margin of the capitulum, at about the level of the anterior part of the nucleus, there seems to originate a narrow membrane, which is turned back as the main capitular membrane. At its origin this flap is less than 2μ wide; it is much narrower than the one in *H. calotermitis.*

A scimiter-shaped, obliquely directed membrane originates in the papillar part of the capitulum and turns around the anterior part of the body (pl. 52, fig. 41). It is broad at its origin and diminishes progressively in width. Its terminal part is situated close to the flap; though somewhat more peripheral in position than the flap, it may be confused with it. The membrane that arises in the papillar region of *H. calotermitis* is not so long, so that confusion with the flap in that species is less likely. No rods or granules are associated with this capitular extension of *H. riciniata;* consequently, it is not so easy to trace its outlines as in *H. insignita* and certain other species.

Interior to the membrane of the main part of the capitulum of the axostyle are some granules (pl. 53, fig. 47) similar to those in *H. calotermitis,* but less numerous and more scattered than in that species.

The anterior part of the trunk of the axostyle is similar in structure to that of *H. calotermitis,* and expands posterior to the nucleus in a similar way. A few granules are grouped in the core of the axostyle posterior to the nucleus. However, no small granules are present in the region between the core and the outer sheath. In that region granules are conspicuous in many specimens of *H. calotermitis.*

The trunk of the axostyle projects in a tapering end for a considerable distance posteriorly (fig. E). Near the posterior end of the cytosome the axostyle is surrounded by a sleeve 4–5μ long, consisting of a thin membrane applied to the axostyle anteriorly and standing out from it posteriorly, since the axostyle tapers and the sleeve remains cylindrical. The sleeve bears a spiral filament similar to that of *H. calotermitis.*

Spirochaetes 5–6$\mu$ long, which are short relative to those on some other species, adhere in a tuft over the capitulum (pl. 53, fig. 46). Similar spirochaetes are adherent to the posterior half or two-thirds of the body. In the region between the two groups of spirochaetes I have not observed any of the peripheral rods or granules that are present in certain other species. There is often some correspondence between the zones of adherent spirochaetes and the inclusions of the cytoplasm. The posterior part where the spirochaetes adhere is often densely packed with wood particles, which occupy the whole region almost to the surface layer. The cytoplasm beneath the spirochaete-free zone is often relatively free of inclusions, either all the way to the axostyle and parabasal body or for a large part of the way. The cytoplasm of this part then appears homogeneous and finely alveolar, with few inclusions of any kind. Sometimes, however, the whole area of cytoplasm, including the region alongside the nucleus and parabasal body, is filled with wood.

A number of polymonad specimens of *H. riciniata* have been found on the slides. The specimens shown on plate 53 are a double animal, with two completely reorganized mastigonts (fig. 46), and a much enlarged cytoplasmic body with seven mastigonts (fig. 48).

### **Hyperdevescovina insignita** sp. nov.

(Pl. 54, figs. 49–51; pl. 55, figs. 52–56; fig. F)

Small form of *Gymnonympha zeylanica*, Dobell, 1910, Spolia Zeylan., 7:81, pl. 11, fig. 2.

*Type host.*—*Neotermes militaris* (Desneux). Ceylon.

T-303. (Cleveland.) (Syntype slides TP-252:5, 6, 9, 10.)

*Diagnosis.*—Length 61 (35–96)$\mu$; width 38 (22–61)$\mu$; anterior flagella of length about equal to that of body; trailing flagellum of similar length and but little thicker; cresta broad triangular with apex at blepharoplast, equal sides, posteromedial edge more or less deeply excavated, length less than 2$\mu$; parabasal body turned around nucleus and axostyle most often 4–7, range 2–13.5 times, first gyre notably wider than next one and separated from it; capitulum of axostyle expanded in broad membranous sheet over anterior end of body, short stout rodlets over membrane; trunk of axostyle stout, tapered gradually posteriorly, sharpened at end to short spike that projects a few microns from posterior end of body; nucleus 8.2 (6–10.5)$\mu \times$ 5.3 (4–6.5)$\mu$; peripheral rodlets in broad zone occupying posterior half to three-quarters of body; spirochaetes 7–10$\mu$ long, adherent to posterior part of body.

The protozoa of *Neotermes militaris* were studied by Dobell (1910), but he did not describe this devescovinid as a separate species. He observed and figured a flagellate that is probably the same species, but he thought it possible that it was a young stage of *Gymnonympha zeylanica.* I have discussed the relationship in my paper on *Trichonympha,* in the account of *T. zeylanica* (Kirby, 1944, p. 200). The flagella of *T. zeylanica* cover a proportion of its body similar to that often occupied by the spirochaetes on *H. insignita.* Dobell apparently mistook the spirochaetes for flagella, and regarded the posterior end as anterior; as a result, he arrived at the opinion that the flagellates might be small forms of *Gymnonympha* in which the nucleus was situated posteriorly.

The details of arrangement of the blepharoplasts and related structures were not clearly demonstrated in the material. Together with the cresta and flagella, these structures are similar to those in *H. caudata.* According to staining conditions, the anterior granule-complex appears as a massive body or as several separate granules. A rhizoplast extends to the nuclear membrane. There is some indication of the existence of the same type of stout filament as that described as an accessory filament in *H. caudata.* Where the roots of the anterior flagella approach the anterior granule-complex, a large, more or less triangular, deep-staining region sometimes appears. This is probably due to overstaining of the flagellar granules and adjacent parts of the capitulum. The short, curved rod in the region of the anterior granule-complex that occurs in some other species was not seen in *H. insignita,* but nevertheless it may be present.

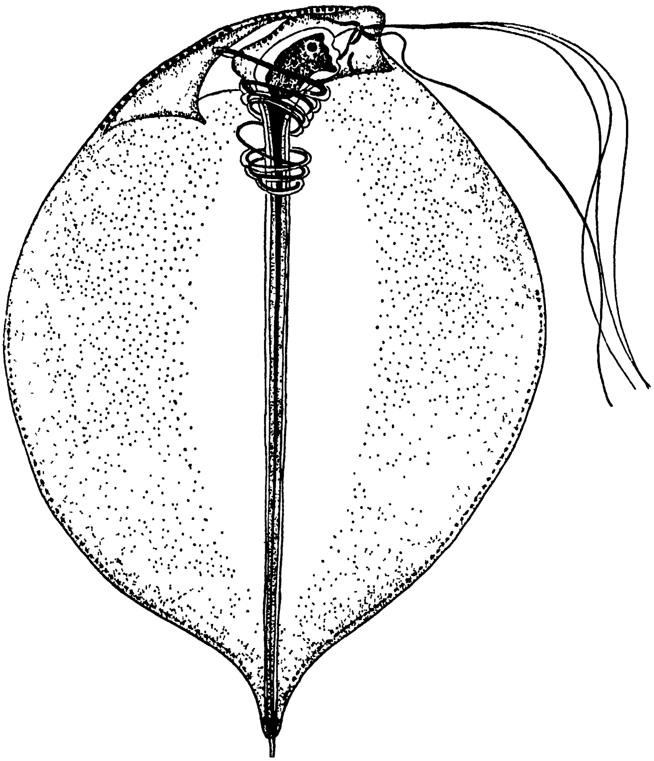

Fig. F. *Hyperdevescovina insignita* sp. nov. from *Neotermes militaris.* Ceylon. Spirochaetes adherent to posterior part of body are omitted. Rodlets on capitular membrane and in belt around body are shown only at edges. See also plate 54, fig. 49. × 1500.

The posterior end of the body is ordinarily somewhat pointed, but sometimes it is broadly rounded. In some specimens on slide preparations, the cytosome had been reduced so that a considerable length of the axostyle extended beyond the main body of cytoplasm. However, except for the short projecting spike, it was still covered by a thin layer of cytoplasm to which adhered the spirochaetes normally present on the posterior part of the body.

The rounded anterior end of the parabasal body is situated close to the nuclear membrane at a distance of several microns from the anterior group of granules, to which it is connected by a filament (pl. 55, fig. 53). No longitudinal anterior limb is present; the parabasal body passes transversely from its origin and begins to coil at once. The first gyre is broad, usually extending to or near the inner side of the capitular membrane. The anterior part of the helix surrounds both the nucleus and the portion of the capitulum alongside of the nucleus. The number of gyres in 50 specimens ranged from 2 to 13.5, 37 having from 4 to 7 turns. The helix usually is close and compact, narrowing with the decreasing diameter of the structure that it surrounds. Not infrequently, however, the regularity of the helix is disturbed by excessive breadth of one gyre, or by the pulling away of part of the gyres from the rest (pl. 55, fig. 53). In a few specimens the posterior part of the parabasal body had a ramus that either was coiled with the main structure or extended into the cytoplasm. In one specimen the parabasal body gave off a ramus at the second turn, but the two parts met again at the fourth turn.

The trunk of the axostyle tapers in some degree, but it remains fairly stout as far as the posterior end of the cytosome (pl. 54, fig. 49; pl. 55, fig. 55). Near the place of projection is a mufflike structure around it (fig. 55); I have observed no series of rings or spiral filament. At the posterior end of the axostyle is a slender, short, projecting spike, which tapers to a point (fig. F). Its length is no more than a few microns. The short projection is in marked contrast to the long ones of *H. calotermitis, H. caudata,* and certain other species.

In heavily stained iron-haematoxylin preparations the entire trunk of the axostyle may be black, or only its posterior part may be stained. In favorably stained material a central chromophile strand or core appears, surrounded by two or three cylindrical sheaths (pl. 54, fig. 49).

The outermost sheath of the axostyle continues in a flattened, capitular expansion flanking the nucleus and extending to the blepharoplast region and into the papilla. This part of the capitulum is on the left side of the nucleus. Its anterior portion is spread into a membranous sheet as broad as the distance between the level of the posterior end of the nucleus and the anterior extremity. The membrane extends over the entire right side, close to the edge of the body, and continues on the ventral and left sides to near the edge of the original anterior extension of the trunk of the axostyle, without narrowing as do the capitular expansions of certain other species (pl. 54, fig. 49; fig. F).

The entire membrane of the capitulum is beset exteriorly with short, stout rodlets that stain readily and deeply with iron-haematoxylin after Schaudinn fixation (pl. 55, fig. 54). The length and number of these rodlets vary, but some are always present (pl. 54, figs. 49–51).

Similar rodlets or granules are present in a layer in the cytoplasm close to the periphery of a large part of the body. The distance of body rodlets from the surface is the same as that of capitular rodlets (pl. 55, fig. 55). The area of body rodlets, like that of capitular rodlets, is sharply delimited at the edge;

a band free of rodlets intervenes between the two zones (pl. 54, fig. 51). The rodlet-free band is narrow in some specimens; in others it extends as far as the middle of the body.

The spirochaetes of the dense group on the posterior part of the body are the only adherent microörganisms (pl. 54, figs, 49, 51; pl. 55, fig. 55). In some specimens the spirochaetes are restricted to a small area immediately around the projecting axostyle. Usually the area occupies the entire terminal surface of the body; occasionally it extends more anteriorly.

A double individual, containing two completely reorganized mastigonts, is represented by figure 56, plate 55. One of the mastigonts is in process of extrusion, and is covered with a minimum amount of cytoplasm. The specimen indicates the possibility that when double individuals are formed, as is not infrequent in devescovinids, one of the mastigonts may sometimes be extruded. Possibly such an extruded mastigont would be able to regenerate a normal cytosome.

### **Hyperdevescovina balteata** sp. nov.

(Pl. 56, *figs.* 57–58; pl. 57, *figs.* 59–62; *fig.* G; *fig.* H)

*Type host.*—*Proglyptotermes spoliator* (Hill) Emerson. Australia.
T-506. (Hill-Cleveland.) Aust. Cap. Terr. (Syntype slides TP-506:1, 2, 9.)

*Diagnosis.*—Length 66 (51–91)μ; width 51 (40–59)μ; trailing flagellum a cord somewhat shorter than body; cresta with two equal arms about 1.5μ long; parabasal body turned around nucleus and axostyle, first turn notably broader than the one posterior to it, 6 (4.5–7) gyres; capitulum of axostyle extended in broad quadrangular membrane on which are rods; trunk of axostyle broad anteriorly, tapering to posterior end of body, after which it diminishes rapidly to spikelike end, 3–4μ long, which usually projects from cytosome; muff about 1μ long around axostyle before projection; nucleus 8.7 (7.4–9.1)μ × 5.5 (4.6–5.7)μ; belt of peripheral rods, often 8–24μ broad, around middle part of body; spirochaetes adherent to whole region of body posterior to band.

At the place of origin of the two flagellar roots of the three anterior flagella, the trailing flagellum, the cresta and the accessory filament, the nuclear rhizoplast, and the small stainable body that extends posteriorly near the point of origin of the nuclear rhizoplast, the complex is similar to that of other species of *Hyperdevescovina.*

The cresta possesses two narrow, posteriorly pointed arms about 1.5μ long. The two arms are equal in size, slightly curved outwardly; the angle between them at the beginning is often about 90°.

The accessory filament is stout in its posterior part, which parallels the posterior margin of the first part of the parabasal body (pl. 56, fig. 57). In the same region the parabasal filament can be seen at the inner margin of the parabasal body, where it lies within the main substance. Subsequently the parabasal filament continues at the inner edge of the parabasal helix, broadening to a band.

The capitulum of the axostyle is expanded in an anterior membrane similar to that of *H. insignita.* Over its entire extent, the anterior peripheral rods are always present in a precise pattern (pl. 57, figs. 59–61). The rods are stained homogeneously with Heidenhain's and Delafield's haematoxylin and are 0.7–1.5μ long. They are shaped like moderately stout bacilli, and are arranged in longitudinal rows, except for some disarrangement at times. The rows that begin at the anterior end of the flagellate spread out considerably as they pass posteriorly. Additional rows, which do not reach all the way anteriorly, are inserted between them; still more posteriorly, other shorter rows may intervene. The shape of the whole group bears some resemblance to that of one valve of a cardium type of pelecypod shell. The papilla of the flagellate is at the position where the beak of the shell would be placed. Around and posterior to the place of origin of the flagella, in an area bounded by a semicircular outline, the rods are absent. The direction of the rows of rods corresponds to the radial sculpture of this type of shell. Some variation occurs in the depth of the bowl and the radius of the rod-free zone. The posterior boundary of the group of rods is fairly sharply defined by a more or less even termination of the rows, but it is not exact. Except around the lateral edges

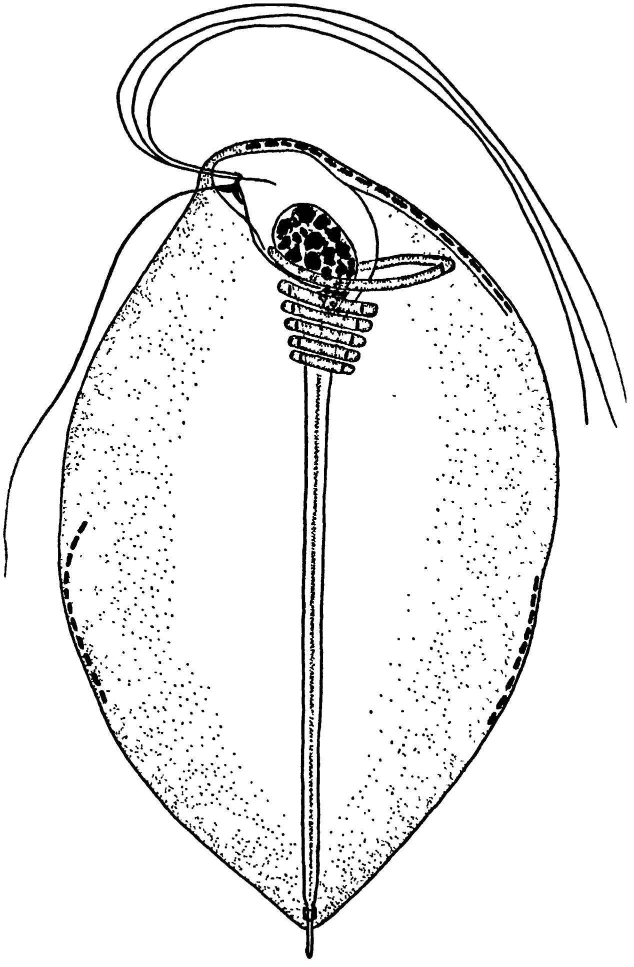

Fig. G. *Hyperdevescovina balteata* sp. nov. from *Proglyptotermes spoliator*. Australia. Spirochaetes adherent to posterior part of body are omitted. See plate 56, fig. 57. × 1500.

of the rod-free zone near the flagella, the rods do not run parallel to the boundary.

The rods are situated just interior to the surface layer of the body, and all lie with their long axes tangential to the surface. Their association is, however, with the underlying membrane rather than with the surface of the body. When in the preparations the cytoplasm has been distorted, sometimes protuberances appear, peripheral to the rods, which then seem to lie deeper in the body.

Underlying the layer of rods is a membrane that is sharply defined at the edges (pl. 56, fig. 57). The rods lie in a clear space between the membrane and the surface of the body; this space contains nothing but the rods. They are separated by a clear zone from the underlying membrane. It is probable that the whole area covered by the rods is occupied by an extended capitular membrane, but indication of the membrane is seen only where it is viewed in optical section at the turns. The membrane is continuous with the main body of the capitulum anterior to the nucleus.

Immediately posterior to the nucleus the axostyle has a diameter of 4 or 5μ in specimens of average size. It is nearly circular in cross section, appearing much the same, whatever the orientation of the flagellate. The part of the trunk that lies within the parabasal helix is conical in form, tapering to a diameter of about 2μ, which the trunk has for most of its length. It tapers gradually as it proceeds posteriorly, until near the posterior end of the cytosome its diameter is about 1.5μ. Then the diameter abruptly decreases, within a distance of about 1μ, to a spikelike form a third or less of the diameter of the trunk preceding it (pl. 56, fig. 58). The spike has a length of 3 or 4μ. It does not become a filament, but keeps the same size for all its length. It may be stained deeply. In some specimens it projects beyond the cytosome, at least for part of its length; the existence of this projection is probably normal, though the spike is entirely enclosed in cytoplasm in many specimens on smears. In some favorably stained flagellates a muff shaped like a napkin ring appears around the proximal part of the spike.

The axostyle has a deep-staining core (fig. G), but I did not observe so complex an arrangement of interior membranes and granules as in some other species. The clavate capitulum is bent toward the crestal region, and the somewhat quadrangular nucleus lies against it or is set into it. An angle of the nucleus lies at the middle of the trunk of the axostyle, and the long axis of the nucleus, seen from the crestal side, bends to the observer's right, at a varying angle, often about 45°.

Around the body in the middle region is a band of peripheral rods that individually are similar to those of the capitular region (fig. G; pl. 57, fig. 59). The position of the band varies: sometimes it is at the middle, sometimes posterior to the middle, less often anterior to the middle. The band is usually of nearly the same width in its course around the body, though some variation occurs. Specimens have been seen in which the band is much broader on one side; in one specimen the band was only two rods wide on one side and covered half the length of the body on the other side. The direction of the rods is in general longitudinal, but they are subject to more displacement with alteration of body form than are those of the capitular region. They tend to be arranged in longitudinal rows, though this tendency is not expressed by exact orderliness in specimens on smears. The rods of larger size are not more than 1.5μ long. In narrow bands, four or five rods may occur in a longitudinal row. Larger flagellates have wider bands; breadths from 8μ to 24μ have been measured.

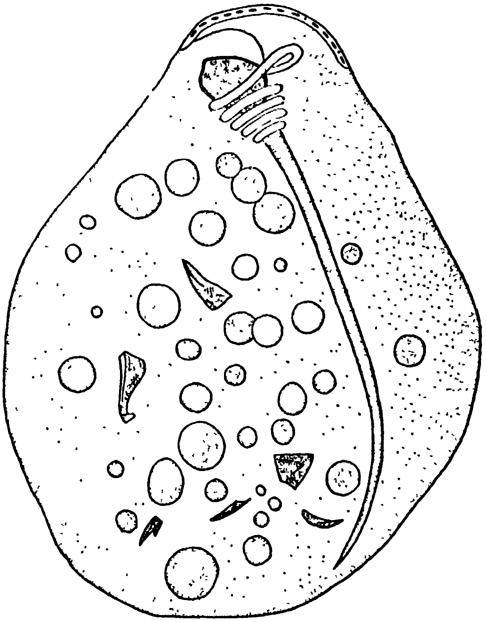

Fig. H. *Hyperdevescovina balteata.* Particles of wood and spherules in cytoplasm. S.D. × 1150.

The position of these rods in relation to the surface layer of the body is similar to that of the anterior rods. In most specimens they are very close to the surface, but they may lie deeper, especially at the anterior end of the band. The band of rods seems to be organized as a unit structure. The rods do not disperse readily in damaged specimens as they would if they were merely enclosed separately in the cytoplasm.

Every specimen examined contained a large amount of inclusions in the cytoplasm. Three kinds of inclusions can be differentiated. Many small angular fragments of wood are present. Among them are spherules (fig. H) that stain gray in iron-haematoxylin. Many specimens have few spherules; in others they are more abundant. They vary greatly in size: a diameter of 1–2μ is frequent, but some spherules range up to 6μ. Each spherule is surrounded by a clear zone, as are the particles of wood. The interior of the spherules may be homogeneous or may show relatively large vacuoles. These structures resemble those that occur in certain oxymonads, and like them they apparently are digestion products derived from wood. The third type of cytoplasmic inclusion consists of granules with a diameter of 1μ or less, occurring isolated or more commonly in groups. They are present in the majority of flagellates, but in varying numbers, interspersed with the wood and the spherules.

The mass of wood, spherules, and granules usually lies in the part of the body posterior to the last part of the parabasal helix. The cytoplasm at the level of the nucleus and the parabasal body seldom contains any large inclusions. The mass may occupy the entire posterior cytoplasm, not even leaving free a peripheral zone of appreciable extent; or there may be an ectoplasm relatively free of inclusions.

The region to which spiral microörganisms adhere usually begins immediately posterior to the band, and extends over all the posterior part of the body (pl. 56, fig. 57; pl. 57, fig. 59). The extent of the area varies with the position of the band.

*H. balteata* closely resembles *H. insignita*. The two species are similar in size, although smaller specimens were present in the material I examined of the second species, so that the range extended lower. The axostyles and parabasal bodies are exactly similar in two; the resemblance extends even to characteristics such as the shape of the capitular membrane, the form and length of the posterior spike, and the position and extent of the wider, separated first gyre of the parabasal. The hosts have been placed in different genera; they are widely separated geographically, and in well-stained material the two forms can be differentiated by certain features. It seems desirable, therefore, to regard them as separate species.

The differences in dimensions are probably not significant, considering the variation that may occur in different hosts and under different circumstances. In *H. insignita* the rods over the capitular membrane are much smaller in size than those of *H. balteata;* many of them appear merely as granules, and the majority are short rods not more than 0.5μ long, whereas in *H. balteata* the length of the rods averages at least twice as much. Rods are more numerous in *H. insignita,* and appear to be in closer contact with the underlying membrane.

The two species differ also in the size and extent of the rods that form a belt around the body. The belt in *H. insignita* usually begins anteriorly at or not far from the level of the parabasal body, and extends to within a short distance of the posterior end. In *H. balteata* it is much narrower, and generally does not extend so far posteriorly; thus the spirochaetes adhere to a larger area. The individual rods of the belt of *H. balteata* are conspicuous, being relatively stout and often about 1.5μ long. Those in *H. insignita* are inconspicuous, and are not more than 0.5μ long.

### **Hyperdevescovina falcifera** sp. nov.

(Pl. 57, fig. 63; pl. 58, figs. 64–68; pl. 59, fig. 69; fig. I)

*Type host.—Proglyptotermes rufinotum* (Hill) Emerson. Australia.

T-503. (Hill 3185.) Aust. Cap. Terr. (Syntype slides TP-503:21, 49, 114, 157.)

*Additional host.—Proglyptotermes banksiae* (Hill) Emerson. Australia.

T-502. (Cleveland-Hill.) Mallacoota, Victoria. (Homosyntype slides TP-502:113, 71, 29.)

*Diagnosis.*—(From type host): Length 53 (39–69)μ; width 30 (22–36)μ; cresta 1.5–3μ long, two arms usually meeting approximately at right angles; parabasal turns 3–4.25, first gyre somewhat but not notably wider than, or separated from, second gyre; membrane extending from capitulum of axostyle falciform in shape, narrowing as it passes around ventral side to left side of nucleus, where it ends bluntly pointed; rods covering this membranous extension, 0.5–1μ long; trunk of axostyle tapered gradually posteriorly, then reduced abruptly to pointed filament projecting usually 5 or 6μ; nucleus 6.8 (6–7.3)μ × 4.3 (4–5.3)μ; belt of peripheral rods around body posterior to middle, leaving free the rounded posterior extremity, to which spirochaetes adhere.

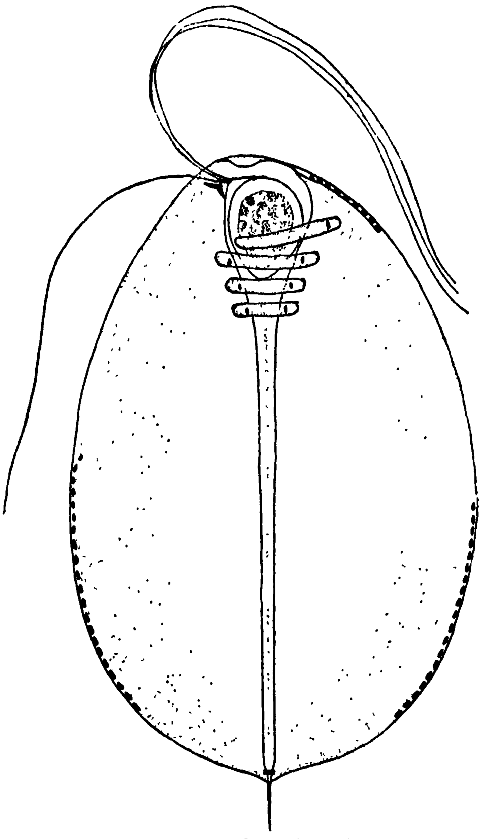

Fig. I. *Hyperdevescovina falcifera* sp. nov. from *Proglyptotermes rufinotum*. Spirochaetes adherent to posterior end of body are omitted. See plate 58, fig. 66. × 1500.

The flagellate faunule of *Proglyptotermes banksiae* is similar to that of *P. rufinotum*. Besides *Hyperdevescovina falcifera,* a species of *Trichonympha* of the *chattoni* type is present in both hosts; and in the two termites is found a small hypermastigote of a unique type that is present in no other Australian termites that I have examined. Hill (1942), in describing *C. banksiae* as a new species, stated that the soldier differs markedly from that of any other described species.

The two arms of the cresta of *H. falcifera* most often meet at approximately right angles, but sometimes they spread at a greater angle. Often the arms are narrow for their whole length; sometimes they are broader toward the point of union. The depth of excavation of the posterior edge varies accordingly.

The complex at the place of origin of the mastigont organelles is like that of other species of the genus. Posterior to the granule that is met by the one of the two roots of the anterior flagella nearest to the cresta is a large elongate granule (pl. 58, fig. 67). The nuclear rhizoplast passes along one side of this large granule. The ventral root of the anterior flagella passes to a position ventral to the large granule, and at its end the specimens studied showed no particular enlargement or granule. A filament connects this place to the granule at the end of the other flagellar root.

The capitulum expanding from the trunk of the axostyle lies in large part on the dorsal side of the nucleus. To the left of the anterior granule-complex it protrudes in a broad lobe. At the right of the complex it gives origin to the membranous extension. The membrane extends transversely around the anterior part of the body, passing around the nucleus first on the right side, then on the ventral side, and partly around on the left, where it ends bluntly pointed. The membrane is broad at its origin, about 6–7μ, but distally it decreases in breadth in a somewhat falciform shape. The anterior surface of the membrane is directed obliquely toward the broad anterior surface of the body. Between its end and the cresta is a gap 7 or 8μ in extent.

The narrow space between the membrane and the surface of the body is occupied in all specimens by rods that are applied to the membrane (pl. 57, fig. 63; pl. 58, figs. 64–68). The thickness of the rods is sufficient to bring them in contact with the bounding layer of the body. They occur only on the membranous extension and not on the main part of the capitulum. Their spacing is regular and their distribution uniform along the edges of the membrane, where they are lined up in regular rows, parallel to one another like ties of a railroad track (pl. 58, fig. 68). On other parts of the membrane the alignment tends to be in similar rows, but is less regular. The individual rods are 0.5–1μ long, are stout for their whole length, and are as broad as elsewhere at their rounded ends.

The trunk of the axostyle tapers gradually from about 3μ posterior to the nucleus to 1μ near the posterior end of the body. It is then reduced abruptly to the very slender, pointed terminal part that projects from the cytoplasm for a few microns (fig. I). Surrounding this slender part before projection is a ring similar to that in *H. insignita* and similar species.

The broad belt of rods in the peripheral cytoplasm of the posterior part of the body often covers the region from the middle to halfway or more from this point to the posterior end (pl. 58, fig. 66). The rods are like those on the capitular membrane. They show a tendency toward arrangement in both transverse and longitudinal rows.

Spirochaetes adhere to the posterior extremity where these rods are not present (pl. 58, fig. 66). In the peripheral cytoplasm of the region to which the spirochaetes adhere are numerous small, deep-staining granules. They are not so close to the surface as the rods, and often some are adherent in a group around the posterior part of the trunk of the axostyle.

Wood particles are abundant in the cytoplasm, and they show the distribution that has been noted in other species of the genus. They are present throughout the region covered by the peripheral rods, and extend to the surface, leaving no wood-free ectoplasm of appreciable extent. In the anterior region is a relatively broad zone of peripheral cytoplasm that is free of wood particles. The cytoplasm here appears rather dense and finely alveolar. In preparations the rod-free region is sometimes swollen out, while the zone with the band of rods is not, so that a groove appears at the beginning of the band (pl. 58, fig. 66).

In *P. rufinotum* a number of double individuals of *H. falcifera* have been seen, with two completely reorganized mastigonts in a common cytosome (pl. 58, fig. 66). In these the capitular rods were in two groups, corresponding to the two membranes, and the cytosomal belt of rods was single. In *P. banksiae* a specimen with nine mastigonts was found (pl. 59, fig. 69).

The closest resemblance of this flagellate is to *H. balteata*. The rods covering the membranous extension of the capitulum are different; they are somewhat smaller in *H. falcifera,* but the difference is not conspicuous and is not certainly a true structural one. The most significant difference is in the shape of the membranous extension of the capitulum, which corresponds to the area covered by the anterior peripheral rods. In *H. balteata* this membrane forms a shell-like cap over the anterior end. In *H. falcifera* it is a falciform structure that passes partly around the anterior end, but leaves free the anterior surface. Its tapering, bluntly pointed form is notably different from that of the wide membrane of *H. balteata*. The terminal part of the axostyle in *H. falcifera* is distinctly unlike that of *H. balteata,* which is shorter and stouter, since it does not diminish to a filament.

### **Hyperdevescovina torquata** sp. nov.

(Pl. 59, figs. 70–71; pl. 60, figs. 72–73; fig. J)

*Type host.*—***Proglyptotermes hilli*** Emerson. Australia.

T-518. (Hill 3491.) S.W. Australia. (Syntype slides TP-518:7, 12, 18.)

*Diagnosis.*—Length 73 (45–105)μ; width 43 (33–66)μ; cresta 2–2.7μ long; parabasal body wound in regular, close-set helix, first gyre not appreciably wider than, or separated by an appreciable distance from, the one posterior to it, turns averaging 10, range 5–15; capitulum of axostyle expanded in membranous extension that covers anterior part of body and lacks overlying rods; trunk of axostyle with short projecting spike similar to that of *H. balteata;* nucleus 8.5 (6.7–10)μ × 5.2 (4.0–7.3)μ; no peripheral rods in belt around body; spirochaetes, many about 10μ long, adherent anteriorly over region of capitular membrane; somewhat shorter spirochaetes adherent in dense coat to posterior half or more of body.

A characteristic feature of this large, stout species is the close, regular winding of the parabasal body (pl. 59, figs, 70, 71). The first turn, unlike that in *Hyperdevescovina insignita,* is applied directly to the following part of the helix and is not appreciably broader than the second turn. The anterior part of the parabasal helix sometimes encloses the nucleus for as much as half of its length. The width of the anterior end of the helix varies from 9μ to 15μ; of the posterior end from 6μ to 7μ. The most anterior part of the parabasal body turns abruptly away from the helix at an angle that often is about half of a right angle (pl. 59, fig. 71). As in other species, the main substance of the parabasal body terminates a certain distance short of the basal granule-complex. In specimens stained with iron-haematoxylin, a well-defined parabasal thread, which is not so much broadened as in certain other species, appears at the inner edge of the helix (pl. 59, fig. 70).

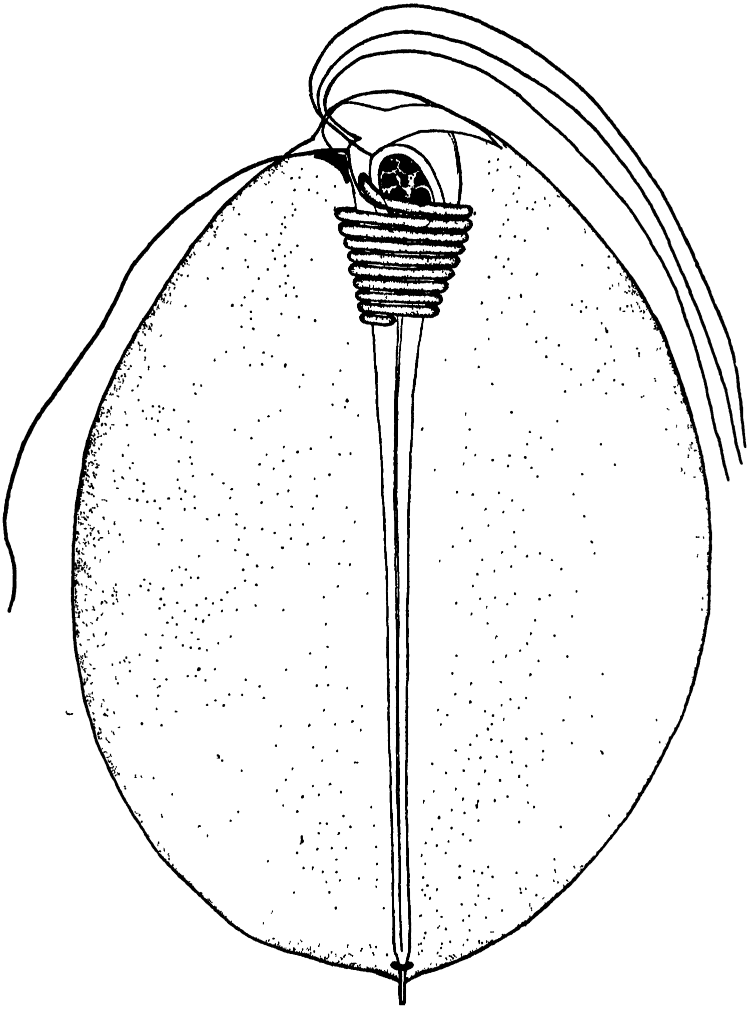

Fig. J. *Hyperdevescovina torquata* sp. nov. from *Proglyptotermes hilli*, Australia. Spirochaetes adherent to anterior end and posterior half or more of body are omitted. See plate 60, fig. 72. × 1500.

The axostyle ends in a short, nonfilamentous spike (fig. J) similar to that of *H. balteata*. It projects for only a few microns from the posterior end. Anterior to its projection, it is surrounded by a ring shaped like a napkin ring.

Spirochaetes are present in abundance on the body surface of this species (pl. 60, figs. 72, 73). Many adhere in a dense group anteriorly over the membranous expansion of the capitulum. Spirochaetes that seem to be somewhat shorter than the anterior ones adhere in a dense coat to the greater part of the surface of the body, including the whole posterior end. Between the two groups of spirochaetes is a region where the surface is free of microörganisms; this region often amounts to about half of the surface (pl. 60, fig. 72).

There are no rods over the capitular membrane and no peripheral rods forming a belt around the body. In the absence of these rods, as well as in the distribution of spirochaetes and the morphology of the capitulum and membranous extension, *H. torquata* resembles *H. riciniata. H. riciniata* differs markedly, however, in the long projection of its axostyle; and in that species the parabasal body is not so broad and regularly wound a helix, and has fewer turns than in *H. torquata.*

Two double flagellates have been found on the slides (pl. 60, fig. 73).

## GENUS BULLANYMPHA KIRBY

### **Bullanympha** Kirby

*Bullanympha* Kirby, 1938, Quart. J. Micr. Sci., 81:14 (type species *B. silvestrii* Kirby).

*Diagnosis.*—Size large, rounded anteriorly and posteriorly, papilla not conspicuous; three long, slender anterior flagella; one trailing flagellum not longer than body; cresta of typical devescovinid form; parabasal apparatus with a proximal part bending in U-form around nucleus, and attached to this a voluminous distal part that is turned around axostyle; capitulum of axostyle slightly developed; trunk of axostyle tapered gradually to filamentous end enclosed in cytoplasm; nucleus relatively small, longer axis oblique, firmly granular chromatic substance filling interior and one or more nucleoli.

### **Bullanympha silvestrii** Kirby

(Fig. K)

*Bullanympha silvestrii* Kirby, 1938, Quart. J. Micr. Sci., 81:14, pl. 2, figs. 14–17, text fig. 1.
*Type host.*—*Neotermes erythraeus* Silvestri. Eritrea. (Xenosyntype slides TP-321:1, 2.)

*Diagnosis.*—Length 100 (50–138)$\mu$; width 63 (35–100)$\mu$; trailing flagellum a moderately stout cord in its middle part, length less than half that of body; cresta 5.8 (4.4–6.1)$\mu$ long, anteromedial edge about 2$\mu$; capitulum of axostyle moderately expanded, expansion entirely anterior to nucleus; trunk of axostyle moderately stout at level of nucleus, tapering gradually within cytosome to filamentous end not projecting from body; parabasal body with a proximal element bending in U-form beside nucleus, then extending transversely or obliquely posteriorly, and a voluminous, compressed distal element that is turned around axostyle 0.5–3.5 times, averaging 2 times; nucleus broadly ellipsoidal, grooved on one side to receive anterior part of trunk of axostyle, chromatin mass finely granular, with one or two deep-staining peripheral nucleoli, nuclear membrane distinct, separated to greater or lesser extent from chromatin mass, size 9.1 (7–10.5)$\mu \times$ 6.5 (5.5–8.5)$\mu$; peripheral granules present beneath surface of whole body; spirochaetes adherent in sparse coat over entire body.

I have already (Kirby, 1938) published an account of this flagellate in as much detail as was made possible by study of the specimens on two slides sent to me by Professor Silvestri.

*Bullanympha* is similar in a number of features to *Pseudodevescovina;* it might be possible, indeed, to make the former genus a synonym of the latter, if one considered the matter from a different point of view from that which I have taken. When *B. silvestrii* is compared to *P. ramosa,* a similarity will be found in general body form and size, flagella, cresta, shape and structure of

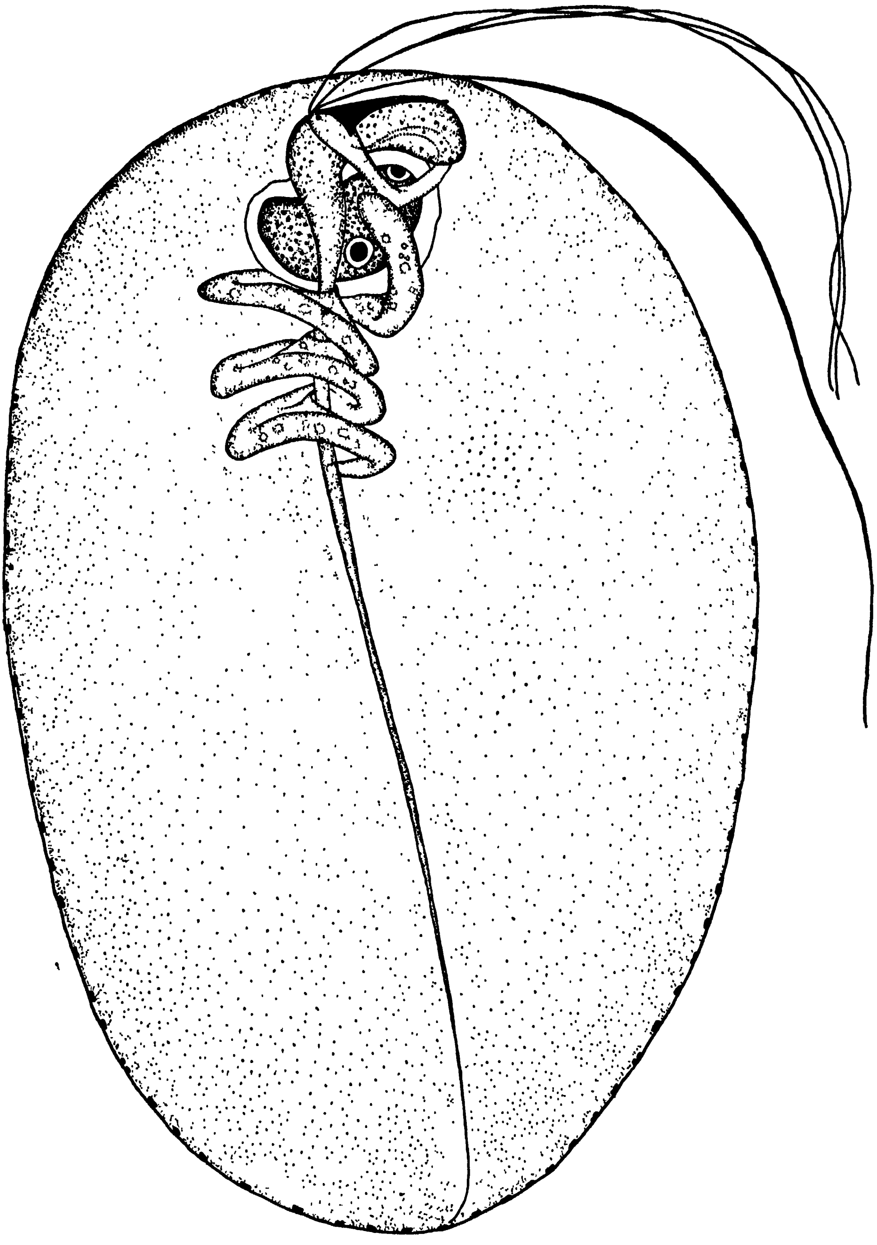

Fig. K. *Bullanympha silvestrii* Kirby from *Neotermes erythraeus*. Eritrea. Adherent spirochaetes omitted. × 1500.

the nucleus, anterior part of the axostyle, and proximal part of the parabasal body. The main differences between the two, so far as the foregoing features are concerned, are the greater size of *Bullanympha* and its organelles.

A striking difference, however, is found in the parabasal body. The parabasal body in *Bullanympha* is unique, though clearly it is a development of the *Foaina-Parajoenia-Pseudodevescovina* type. *Parajoenia* is distinguished from *Foaina* mainly by its distinctive parabasal apparatus, and *Bullanympha* may be differentiated from *Pseudodevescovina* on comparable grounds.

The group of cordlike rami of the parabasal body of *P. ramosa* tends to turn around the axostyle posterior to the nucleus. In *B. silvestrii* this group of rami is replaced by a single, much-inflated structure that turns around the trunk of the axostyle in a regular manner, giving the appearance of a spiral shelf (fig. K).

The trunk of the axostyle of *B. silvestrii* resembles that of *Devescovina* and *Caduceia* rather than that of *Foaina* and *Pseudodevescovina.* In all other respects the flagellate belongs to the *Foaina* group.

## UNDESCRIBED OR UNRECORDED SPECIES

### **Foaina inflata** sp. nov.

(Pl. 61, figs. 79–80; pl. 62, figs. 81–85; fig. L)

*Type host.*—*Neotermes* sp. nov. El Salvador.

T-541. Cerro del Aquila, Dept. Santa Ana. (Syntype slides TP-548 :5, 7, 13, 17.)

T-546. Volcan de Santa Ana, Dept. Santa Ana. (Xenosyntype slide TP-553 :3.)

*Diagnosis.*—Length 55 (44–69)$\mu$; width 25 (23–28)$\mu$; anterior flagella 50–60$\mu$ long; trailing flagellum a moderately stout cord 55–70$\mu$ long; cresta 12–22$\mu$ long, anteromedial edge 3.2–3.5$\mu$; parabasal body consisting basically of V-shaped element embracing nucleus, with long ventral limb, and dorsal limb extended ventrally and transversely in a haematoxylin-staining filament that reaches edge of body, both limbs or dorsal limb commonly inflated in branched or vesicular form; capitulum of axostyle moderately developed, without appendages; trunk of axostyle moderate in size, tapered gradually posteriorly, projecting to filamentous end 6–18$\mu$ long; nucleus 7.4 (5.7–9.1)$\mu \times$ 4.6 (3.4–6.3)$\mu$, form ellipsoidal with long axis more or less in longitudinal axis of body; granules and rods present on capitulum; spirochaetes adherent to most anterior part of body in region of capitulum, no adherent spirochaetes elsewhere.

The notable feature of this species is the remarkable parabasal body (pl. 62, figs. 81–85), which is inflated in form; hence the trivial name *inflata* has been chosen. It appears at first glance to be much unlike the parabasal body that is usually found in devescovinid flagellates. Close study, however, reveals the fact that it is comparable to the parabasal body of *Foaina gracilis, F. signata,* and other species, but that it is developed in an extraordinary manner. Some species have outgrowths from the basic, more or less C-formed main part of the parabasal body; but *F. inflata* displays an enlargement and vacuolization of the substance of the basic structure itself.

The basic part of the organelle is curved around the nucleus, with an anterior V-shaped part, at the apex of which is the blepharoplast, and an extension of the dorsal limb that passes transversely and ventrally (pl. 62, fig. 81). Inflation may involve only the dorsal limb of the V and the posterior transverse part (pl. 62, fig. 84), or it may involve the ventral limb of the V also (pl. 62, fig. 82). Irregular outgrowths from the posterior part of the dorsal limb may occur (pl. 62, fig. 83); and the distal ends of these rami may unite with other outgrowths on the basic structure. The result is a very irregular structure, which appears highly vacuolate or in places fenestrate. The vacuolate appearance is particularly marked in protein-silver impregnations; in these the substance is divided by deeply impregnating walls into clear cells of highly variable size and shape (pl. 62, figs. 82–85). The vacuolated appearance can be seen also in Ehrlich-stained parabasals (pl. 62, fig. 81). Iron-haematoxylin preparations do not show the parabasal well; it can be made out as a gray-stained substance, the outlines of which are usually rather obscure (pl. 61, figs. 79–80). However, in Heidenhain preparations a deep-staining filament appears along the margin of parts of the structure. A filament passes along the dorsal limb parallel to the anteromedial edge of the cresta, and a filament is especially conspicuous along the transverse part posterior to the nucleus. The latter filament continues beyond the substance of the parabasal body, approaching the edge of the body on the ventral side or turning posteriorly in this region.

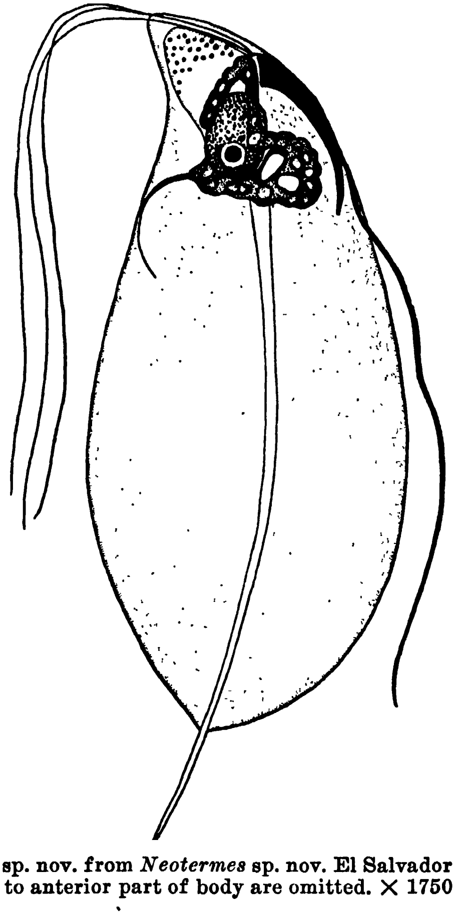

Fig. L. *Foaina inflata* sp. nov. from *Neotermes* sp. nov. El Salvador. Spirochaetes adherent to anterior part of body are omitted. × 1750.

In specimens of average size the diameter of the trunk of the axostyle (fig. L) in the middle part of the body is about 1$\mu$; it is little broader than that at the level of the posterior end of the nucleus. Anteriorly the axostyle is expanded in a spatulate form, but with no special elaboration of the capitulum. The capitulum in the region alongside of and anterior to the nucleus contains an incrustation of granules and small rods. At least some of these seem always to be present in *Foaina inflata,* but they vary in number.

### **Foaina serrata** sp. nov.

(Pl. 61, figs. 74–78; fig. M)

*Type host.*—*Neotermes* sp. nov. El Salvador.

T-546. Volcan de Santa Ana, Dept. Santa Ana. (Syntype slides TP-553:4, 6.)

T-541. Cerro del Aquila, Dept. Santa Ana. (Xenosyntype slides TP-548:2, 16.)

*Diagnosis.*—Length 46 (39–53)μ; width 22 (17–30)μ, broad and truncate at anterior end, papilla at one side; anterior flagella 23–35μ long; trailing flagellum 48–66μ long, a moderately stout cord in its middle part; cresta 9–14μ long, anteromedial edge 1.5–2μ, shape similar to that of *Devescovina lemniscata;* parabasal body forming loop, closed posteriorly, around dorsal end of nucleus, then extended to region anterior to nucleus and turned sharply ventrally in a V; parabasal body in part bordered by a filament, stout and deep-staining in some parts, filament beginning at blepharoplast, following sigmoid course to reach dorsal anterior part of body, then passing across body anterior to nucleus to ventral region, and curved dorsally; beyond sigmoid part this filament is bordered by serrate membrane extending above surface of body; capitulum of axostyle moderately developed; trunk of axostyle stout, enlarged in a cusp posteriorly, surrounded by a muff, and projecting from posterior end 9–14μ; nucleus 6.9 (5.7–10.3)μ × 4.6 (3.4–5.7)μ, longer axis more or less transverse, outline somewhat asymmetric, often concave posteriorly; spirochaetes about 10μ long, adherent in dense mass to anterior part of body; spirochaetes, many 10–15μ long, adherent to all parts of rest of body.

The shape of the body is a characteristic feature of the species. Anteriorly it is broad and rather flat (pl. 61, fig. 74), with a marked overhang on one side where the papilla projects. Posteriorly the body tapers to a narrow end, from which the axostyle, which is stout at that point, extends for a short distance (fig. M).

The parabasal body is an unbranched structure with a form similar to that of *Foaina reflexa,* which is much smaller in size. The part closest to the blepharoplast is at the base of a U-shaped part, the open end of which is directed more or less anteriorly (pl. 61, figs. 76–78). Near the blepharoplast is a sharp angle, often about 90°. A fairly straight limb extends anteriorly from this angle along the dorsal margin of the nucleus to the level of the anterior end of the nucleus; this limb corresponds to the anterior part of the parabasal body in other species. On the other side of the angle near the blepharoplast, the parabasal passes transversely, often for a distance of 5 or 6μ, then extends anteriorly and dorsally, crossing the other limb on the right side in most specimens, and entering the dorsal papillary extension of the body. Near the anterior margin of the body it bends ventrally in a sharp angle and continues near the anterior edge for 4 or 5μ, then ends bluntly.

The parabasal body is of nearly equal stoutness for most of its length, and, with some exceptions, its substance stains deeply with Ehrlich's haematoxylin. The most regularly present of the interruptions is in the posterior, transverse part of the loop, just ventral to the angle near the blepharoplast. Here the parabasal body appears slender, and usually stains lightly or not at all in alum-haematoxylin; then, at first glance, it appears to consist of two parts. This interruption varies in extent, though in most specimens it is present in some degree (pl. 61, figs. 76–78). The parabasal body appears somewhat vacuolated, and is more or less irregular in outline.

The most notable feature of the animal is a stainable, serrate band that originates at the blepharoplast, extends to and along the anterior border of the body, and, after reaching the ventral edge, curves back and dorsally for a short distance (pl. 61, fig. 74; fig. M). The first part of this structure appears as a stout, deep-staining (with iron-haematoxylin) filament, which lies on the dorsal side of the nucleus and is sigmoid in form (pl. 61, fig. 75). In the middle part of the S the filament is broadened in a band form. Beyond the sigmoid bend the structure is differentiated into two parts. There is a siderophile band similar to that of the S, peripheral to which is a more or less clear zone, and at the boundary is a filament that is incurved and pointed in a series of denticles (fig. M). The denticles often number 15–20, and seem to project above the surface of the body. On some haematoxylin-stained slides the serrate filament does not appear; on others and on protargol-impregnated slides it is distinct.

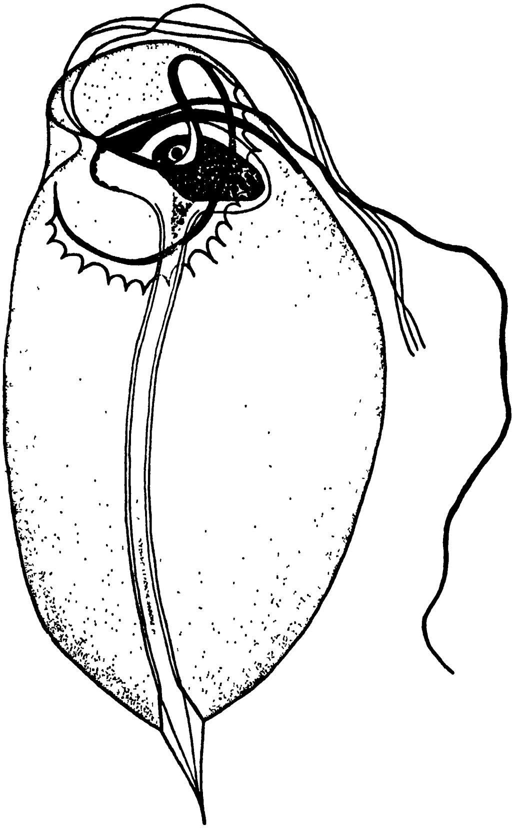

Fig. M. *Foaina serrata* sp. nov. from *Neotermes* sp. nov. El Salvador. Spirochaetes adherent to all parts of body are omitted. × 1750.

This band, in its sigmoid part, is applied to the main substance of the parabasal body. After leaving the blepharoplast it passes along the anteromedial edge of the cresta, then follows the parabasal body into the papilla. It extends far beyond the substance of the parabasal. It is evidently homologous with filaments that have been described in other devescovinids but are much confused in nomenclature. The "parabasal filament" of *Foaina reflexa* (Kirby, 1942*a*, p. 209) is doubtless homologous; but there is considerable doubt whether the structure in *F. serrata* should be regarded as a parabasal filament. It is likely that the "paracrestal filament" in *Macrotrichomonas pulchra* (Kirby, 1942*b*, p. 118) is a homologue; that flagellate also contains a parabasal filament. The structure named "crestal accessory" in *Caduceia monile* may be comparable. Each of these terms seemed suitable for the structure in the flagellate in which they were first named, but if they are homologous, the nomenclature should be revised to give it general applicability. It is possible that the so-called parabasal filament in certain Trichomonadidae is comparable, so that a term including the word "cresta" is not desirable. There is not always a direct relationship to the parabasal body. "Accessory filament," though not connoting any specific relationships, is probably suitable until more is known about the structure.

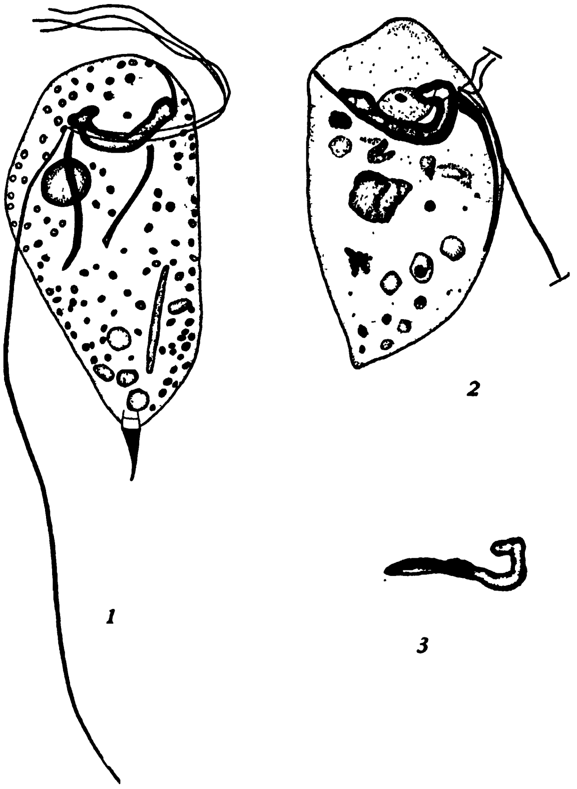

Fig. N. *Foaina reflexa* sp. nov. from *Calcaritermes* sp. nov. El Salvador. × 1800. Specimens do not have loop of parabasal body around dorsal end of nucleus that often occurs in the species. Parabasal body shown as impregnated by silver. Filament extended from distal end in 1 and 2, seen from another aspect as in 3, appears as a band. B.Prot.

### **Foaina reflexa** Kirby

(Fig. N)

*Additional hosts.*—

*Calcaritermes nigriceps* (Emerson). British Guiana. Kartabo. (Emerson.) (Homosyntype slide TP-588:3.)

*Calcaritermes* sp. nov. El Salvador.
T-545. Volcan de Santa Ana, Dept. Santa Ana. (Homosyntype slides TP-552:17, 19, 1.)
*Calcaritermes* sp. nov. El Salvador.
T-548. Chilata, Dept. Sonsonate. (Homosyntype slide TP-555:16.)

The characteristics of the flagellate in *Calcaritermes* T-545 may be summarized as follows: length 26 (18–30.5)μ; width 15 (11.5–19.5)μ; three anterior flagella 23–27μ long; trailing flagellum a moderately stout cord 44–57μ long; cresta 10–15.5μ long; axostyle continued posteriorly in tapered projection 3–5μ long; nucleus 4.6–5.7μ × 2.8–3.4μ; no adherent microörganisms.

In some specimens the parabasal body does not have so marked a loöp passed around the dorsal end of the nucleus as was indicated in the type material. It may extend more transversely, often bending somewhat anteriorly, in the form of a hook or handle. The filament, which extends a few microns beyond the end, and may be turned posteriorly at the periphery of the body, appears as a broader band in silver-impregnated specimens (fig. N).

In these specimens the parabasal body has considerable resemblance to that in *Foaina funifera* and *F. falcifera*. In *F. falcifera* many specimens occur in which the parabasal body has a sigmoid form, the distal part being curved posteriorly. I did not observe this form of parabasal in the specimens of *F. reflexa*. The trailing flagellum is stouter than that of *F. falcifera*. *F. funifera* has a stouter trailing flagellum and a somewhat larger and more slender projecting part of the axostyle; it differs from *F. reflexa* also in the elongated, narrow nucleus, which often is markedly curved in a transverse direction.

### **Foaina nana** (Kirby) Kirby

(Fig. O)

*Additional hosts.*—
*Calcaritermes* sp. nov. El Salvador.
T-545. Volcan de Santa Ana, Dept. Santa Ana. (Homosyntype slides TP-552:7, 21.)
*Calcaritermes* sp. nov. El Salvador.
T-548. Chilata, Dept. Sonsonate. (Homosyntype slide TP-555:12.)
*Calcaritermes brevicollis* (Banks). Panama.
T-233. Taboga Island. (Homosyntype slide TP-144:1.)
*Calcaritermes emarginicollis* (Banks). Costa Rica.
T-171. Estrella. (Homosyntype slide TP-106:2.)
*Calcaritermes nearcticus* Snyder. Florida.
T-535. Ortega. (Homosyntype slide TP-540:9.)
*Calcaritermes nigriceps* (Emerson). British Guiana.
Kartabo. (Emerson.) (Homosyntype slide TP-588:9.)
*Cryptotermes cubicoceps* Emerson. British Guiana.
Kartabo. (Emerson.) (Homosyntype slide TP-585:5.)
*Rugitermes magninotus* Emerson. British Guiana.
Kartabo. (Emerson.) (Homosyntype slide TP-590:16.)

Along with specimens of *Foaina reflexa,* species of *Calcaritermes* include smaller forms of *Foaina* that appear distinctly different, and correspond to *F. nana* in the structure revealed by iron-haematoxylin. The general plan of organization of the two groups of *Foaina* is similar, but there are definite differences which, in the material I examined, did not appear to be connected by transitional forms. Consequently, they are here treated as two species; further study of these, as in certain other described species of *Foaina,* may possibly show that they should be regarded as the same species.

The smaller species of *Foaina* has a cresta that is similar in shape and size to that of the large one. The size of the cytosome being less, the cresta often reaches to, or nearly to, the posterior end.

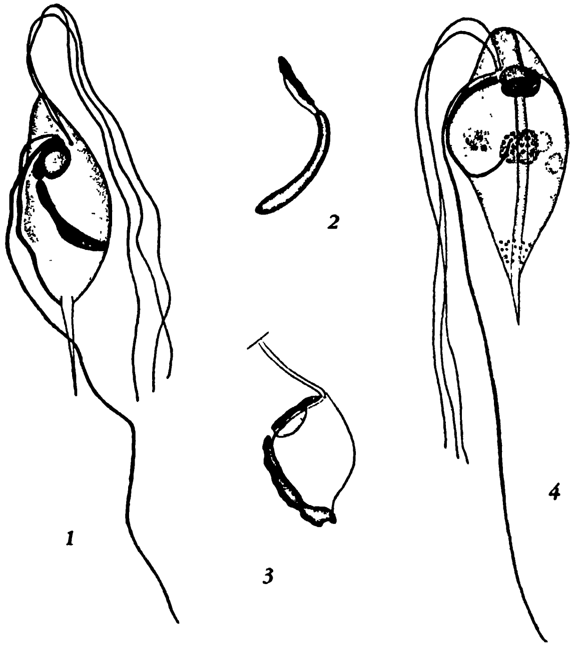

Fig. O. *Foaina nana* Kirby from *Calcaritermes* sp. nov. El Salvador. × 1800. 1–3. Parabasal apparatus, including long, band-shaped posterior structure. B.Prot. 4. Parabasal body with posterior filament as stained in iron-haematoxylin. Same structure in silver-impregnated material is the band. B.H.

The parabasal body is a straight or somewhat curved bacilliform structure, often 3–4$\mu$ long, that lies on the dorsal side of the nucleus and begins in the blepharoplast region. In certain aspects it appears as an elongated ring, the edge impregnated by silver and the interior more clear.

Much more conspicuous than the parabasal body is a band-shaped, somewhat unevenly margined structure that extends at the periphery of the cytosome, generally posteriorly from the posterior end of the parabasal body (fig. O, 1–3). Its length is two or more times that of the part of the parabasal body adjacent to the nucleus, and its breadth is 1 or 2$\mu$, which is also greater than that of the anterior parabasal structure. It impregnates deeply at its edges with silver, and gives much the same reaction and shows the same differentiation of outer black and inner paler structures as the anterior parabasal structure. This impregnatable structure extends as far as, or nearly to, the posterior end of the parabasal, but it does not directly meet the parabasal. Instead, there is a paler and slender filament paralleling the posterior border of the parabasal and passing to the region of the blepharoplast (fig. O, 3). This structure appears to be separate from the parabasal. It is homologous with the serrate band of *F. serrata.*

In iron-haematoxylin material this structure appears as a stout filament (fig. O, 4), tapered posteriorly, as illustrated in my previous descriptions of *F. nana.* The form that it seems to have in these preparations is very different from that which appears in protargol preparations. No silver impregnations of *F. nana* from the type host have been available for study; but since the flagellates appear the same in *Calcaritermes* sp. and in *Cryptotermes hermsi* in preparations made by the same technique, they are provisionally regarded as identical.

Flagellates with the same characteristics as that described above have been found in silver preparations from *Calcaritermes nearcticus* and in iron-haematoxylin preparations from *Calc. brevicollis* and *Calc. emarginicollis.*

### **Foaina hamata** Kirby

*Additional hosts.*—

*Glyptotermes hospitalis* Emerson. British Guiana.
Kartabo. (Emerson.) (Homosyntype slide TP-586:2.)
*Neotermes* sp. nov. El Salvador.
T-541. Cerro del Aquila, Dept. Santa Ana. (Homosyntype slide TP-548:13.)

Specimens from *Glyptotermes hospitalis* ranged in length from 22μ to 32μ. Adherent spirochaetes were abundant on the posterior part of the body, and often extended over the posterior half. Some adherent spirochaetes were also present on the anterior half of the body.

In specimens from *Neotermes* sp. nov. the cresta was 7–9μ long, with an anteromedial edge of about 1.5μ. They corresponded in dimensions and structure to *Foaina hamata* from the type host, except that the projection of the axostyles in some specimens was greater, reaching 20μ and longer. Many specimens had axostylar projections falling within the range of material from the type host; so that fact is not here used for systematic differentiation. Spirochaetes were present on the surface of the body, especially in the posterior part.

### **?Foaina acontophora** Kirby

*Additional hosts.*—

*Glyptotermes guianensis* Emerson. British Guiana.
Kartabo. (Emerson.) (Homosyntype slide TP-580:4.)
*Glyptotermes perparvus* Emerson. British Guiana.
Kartabo. (Emerson.) (Homosyntype slide TP-582:12.)

In a number of ways the species does not correspond to typical *F. acontophora.* It does not develop so large a size, and the trailing flagellum is not so stout. It has a cresta of similar character, however. The material available was not adequate for complete diagnosis. The flagellate may be placed with *F. acontophora* pending further study.

### **Foaina solita Kirby**

*Additional host.*—*Eugitermes magninotus* Emerson. British Guiana.
Kartabo. (Emerson.) (Homosyntype slide TP-590:13.)

## **Foaina grassii** Duboscq & Grassé

*Additional host.*—*Neotermes* sp. nov. El Salvador.
T-541. Cerro del Aquila, Dept. Santa Ana. (Homosyntype slide TP-548:12.)

This flagellate has been identified with *F. grassii* because of the very short cresta, measuring less than 3μ; the moderately stout and very long trailing flagellum; and the axostyle with a projection of moderate length and no notable enlargement before projection. As in the species from the type host, no adherent microörganisms are present.

## **Devescovina cuneata** sp. nov.

(Fig. P)

*Type host.*—*Neotermes* sp. nov. El Salvador.
T-541. Cerro del Aquila, Dept. Santa Ana. (Syntype slides TP-548:6, 8, 15.)
T-546. Volcan de Santa Ana, Dept. Santa Ana. (Xenosyntype slide TP-553:2.)

*Diagnosis.*—Length 47 (34–63)μ; width 14 (10–17)μ; trailing flagellum a stout cord or flattened in very narrow band about 50μ long; anterior flagella 30–43μ long; cresta 2.5–4.4μ long, anteromedial edge 1.5–2μ; parabasal body turned around axostyle one to four times, more than two exceptional; nucleus 5.7 (4.6–6.9)μ × 3.4 (2.9–4.0)μ, central chromatin mass often quadrangular in outline; slender, striation-forming microörganisms present on surface; no adherent spirochaetes.

The parabasal body has a longitudinal limb that runs along the dorsal border of the nucleus for its whole length. At the posterior end of the nucleus the structure bends sharply transversely and turns around the trunk of the axostyle one or more times (fig. P, 2–3). An appreciable distance, which often is about half the thickness of the parabasal substance, separates the gyres in most instances, but this varies. Especially when more than two gyres occur, successive turns may be very close together.

At the anterior end of the nucleus the short terminal part of the parabasal is bent transversely or at a sharper angle. This part may be somewhat enlarged, but is not always so. The longitudinal limb of the parabasal is somewhat flattened against the nucleus (fig. P, 2). The posterior end is rounded and usually is as stout as the rest. The average thickness of the parabasal is about 1μ.

The cortical part of the parabasal body impregnates deeply in protargol, and the interior remains clear. In protargol preparations the structure seen in optical section shows two black borders separated by a more or less clear strip, which is usually about the same thickness as the impregnated bands.

The chromatin mass of the nucleus has an angular form (fig. P, 1). In many specimens its outline is rectangular. In others it is broader in its posterior part than in its anterior part, so that it has a somewhat triangular outline. The posterior border of the chromatin mass is sometimes concave. A deep-stained spherule of variable size is often visible in the clear zone between the chromatin mass and the nuclear membrane. Sometimes it lies against the mass and sometimes it is distinctly separated from it. Often it is posterior to the mass, but its position is variable. This spherule appears to be the nucleolus. Within the chromatin mass, as seen in well-destained material, are deep-stained chromatin blocks of varied size and shape; this type of nucleus is characteristic of the genus *Devescovina.*

*Devescovina cuneata* has some resemblance to *D. cometoides, D. exilis,* and *D. parasoma.* It is distinctly different from all other described species of the genus.

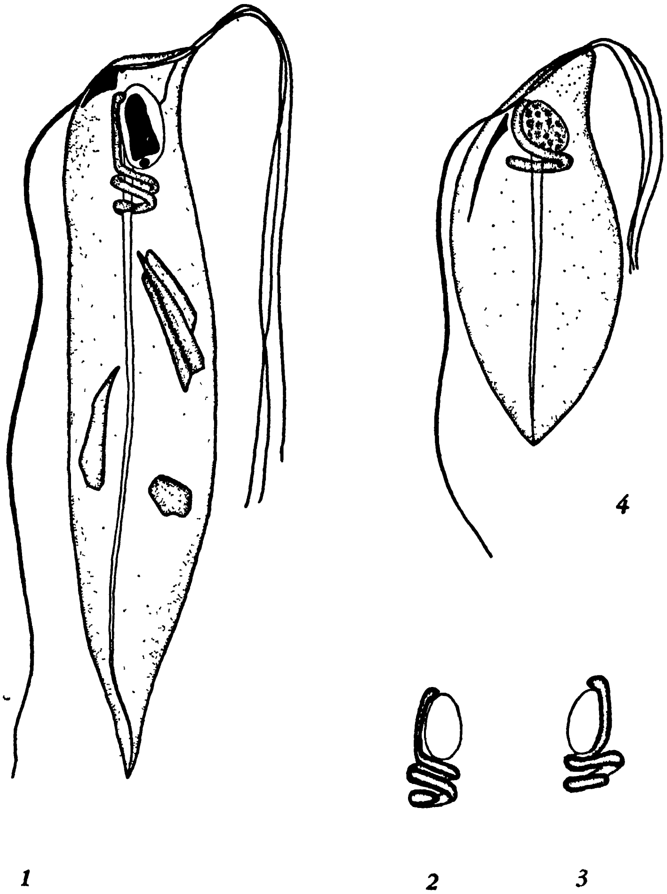

Fig. P. 1–3. *Devescovina cuneata* sp. nov. from *Neotermes* sp. nov. El Salvador. 1. × 2000. 2 and 3. Forms of parabasal body. 4. *Devescovina minor* sp. nov. from *Glyptotermes perparvus.* British Guiana. × 2000.

In *D. cometoides* the trailing flagellum is similarly a stout cord or sometimes a narrow band, the cresta is small, the axostyle is filamentous in its posterior part, and the parabasal body has a similar number of turns. There are definite, though small and not altogether constant, differences. The most significant is the shape of the cresta. The length is a little greater in *D. cuneata* than that typical of *D. cometoides,* but the most significant difference is in shape. In *D. cometoides,* as noted in the key (Kirby, 1941, p. 24), the anteromedial and posteromedial edges are nearly equal in length; in *D. cuneata* the latter is longer. Adherent spirochaetes are present on the former species but not on the latter.

A cresta that is similar in size and shape to that of *D. cuneata* is present in *D. exilis*. That of *D. exilis* is typically more markedly incurved posteriorly, as indicated in plate 5, figure 39. The trailing flagellum is more definitely and regularly shaped like a narrow band in *D. exilis,* and the parabasal body in that species is not so closely wound and does not have so many turns as that of *D. cuneata.*

*D. parasoma* has a cresta of similar shape but somewhat larger size (length 4.4–6.0μ, anteromedial edge 2–2.5μ). The parabasal body has no more turns than the maximum number in *D. cuneata,* the spiral is more regularly closely wound, and the occurrence of more than two turns is most frequent. The axostyle of *D. parasoma* is stouter in its posterior part, and the covering of spirochaetes is also a distinctive feature of that species from *Neotermes tectonae.*

### **Devescovina minor** sp. nov.

(Fig. P, 4)

*Type host.—Glyptotermes perparvus* Emerson.
Kartabo, British Guiana. (Syntype slides TP-582:5, 7.)
*Additional host.—Glyptotermes guianensis* Emerson.
Kartabo, British Guiana. (Homosyntype slide TP-580:3.)

*Diagnosis.*—(From type host): Length 26 (19–34)μ; width 12 (8–18)μ; trailing flagellum a moderately stout cord; cresta 6–9μ long, anteromedial edge 1–1.5μ; parabasal body turned moderately widely around axostyle just posterior to nucleus, about one turn or very little more, occasionally up to two; nucleus 4–5μ × 2.5–4μ; no adherent spirochaetes.

In length and shape the cresta of this species is similar to that of *D. uniflexura,* but the anteromedial edge may be shorter; *D. uniflexura* is much larger and has a ribbon-shaped trailing flagellum.

Use of the key to the species of the genus (Kirby, 1941, pp. 24–25) would lead to *D. tendicula* and *D. coghilli,* with *D. glabra* being close. *D. coghilli* is much longer and, at the same time, narrower, so that its form is far more slender; and the cresta is somewhat shorter. *D. tendicula* is easily differentiated by its very much larger size, by its cresta with a much longer anteromedial edge, and by the distinctive form of its parabasal body. In *D. glabra,* also, the size is greater; the cresta is broader anteriorly and relatively shorter; and the parabasal body has more turns, almost never having as few as one.

### **Devescovina lepida** Kirby

*Additional hosts.—*
*Calcaritermes nigriceps* (Emerson). British Guiana.
Kartabo. (Emerson.) (Homosyntype slide TP-588:10.)
*Calcaritermes* sp. nov. El Salvador.
T-548. Chilata, Dept. Sonsonate. (Homosyntype slide TP-555:8.)

A correction should be noted in the diagnosis of *D. lepida* from the type host (Kirby, 1941, p. 51). The maximum length is misprinted as 39μ; it should be 69μ.

*D. lepida* was not found in a series of preparations made from one colony of *Calcaritermes* sp. nov. T-545 made at Volcan de Santa Ana, El Salvador.

### Caduceia kofoidi sp. nov.

(Fig. Q, 1–4)

*Type host.—Glyptotermes guianensis* Emerson.
Kartabo, British Guiana. (Syntype slides TP-580:1, 2, 5, 9.)
*Additional host.—Glyptotermes perparvus* Emerson.
Kartabo, British Guiana. (Homosyntype slides TP-582:1, 2.)

*Diagnosis.*—Length 71 (46–81)μ; width 33 (24–42)μ; trailing flagellum a moderately stout cord, length less than half that of body; cresta: external edge 3–4μ long, posteromedial edge almost same length, anteromedial edge deeply concave, about 2μ across points; parabasal body slender, turned closely around posterior part of nucleus and axostyle in 4–5 gyres, apparatus bowl-shaped; capitular extension around nuclear region covered by close-set rods; trunk of axostyle not very stout, without internal differentiation, projects 0–6μ in sharpened end; bowl-shaped transverse mass of granules a short distance posterior to parabasal body, surrounding axostyle, deeply siderophile band around trunk of axostyle within granule mass; nucleus ellipsoidal, longer diameter transverse, size 5–5.5μ × 7–8.5μ; peripheral rods over most of body, except for narrow clear band posterior to capitular granules, and often posterior region around projecting axostyle; no adherent microörganisms.

The anterior end of the body is rounded, and an indentation occurs near it on one side, but there is no papilla extended in a point. The flagella emerge from the rounded anterior protuberance (fig. Q, 1).

The posterior end is rounded more or less broadly in the specimens I have examined, and it may or may not be extended in a protuberance where the axostyle projects.

Close to the anterior edge of the nucleus is a pair of granules (fig. Q, 4), which are placed in a direction oblique to the longitudinal axis of the body. Each of the granules gives origin to one of the two roots of the anterior flagella. These filaments pass parallel to one another, and are rather distantly separated in their course through the cytoplasm of the anterior part of the body, deep within it, before becoming free as the three anterior flagella. The filaments in the cytoplasm extend more or less transversely, arched anteriorly.

The cresta (fig. Q, 2) is relatively short and its shape is unusual. In most devescovinid crestas the posteromedial edge is somewhat concave, at least in the anterior part, but in *Caduceia kofoidi* that edge is somewhat straight and is nearly as long as the external edge. The posterior angle is about 45°, so that the two anterior angles are more widely separated in relation to the size of the cresta than is true in most devescovinids. The anteromedial edge is sometimes deeply concave.

In the anterior part of the body is a broad membranous extension of the capitulum, over which there is a caplike layer of rods about one micron long. The rods are close-set, and are arranged in rows both parallel to one another and end to end (fig. Q, 1, 3, 4). In the form of this membrane and the arrangement of the rods *C. kofoidi* is similar to certain species of *Hyperdevescovina.* The anterior part of the body is rather narrow, so that even in its posterior part the cap of rods does not spread out very widely beyond the nucleus, which it partly encloses.

Posterior to the capitular group of rods is a narrow belt where rods are absent; but, posterior to this, all the periphery of the body, except often for the extreme posterior end, is occupied by a layer of rods and granules (fig. Q, 3). The rods resemble those of the anterior cap, but are somewhat larger.

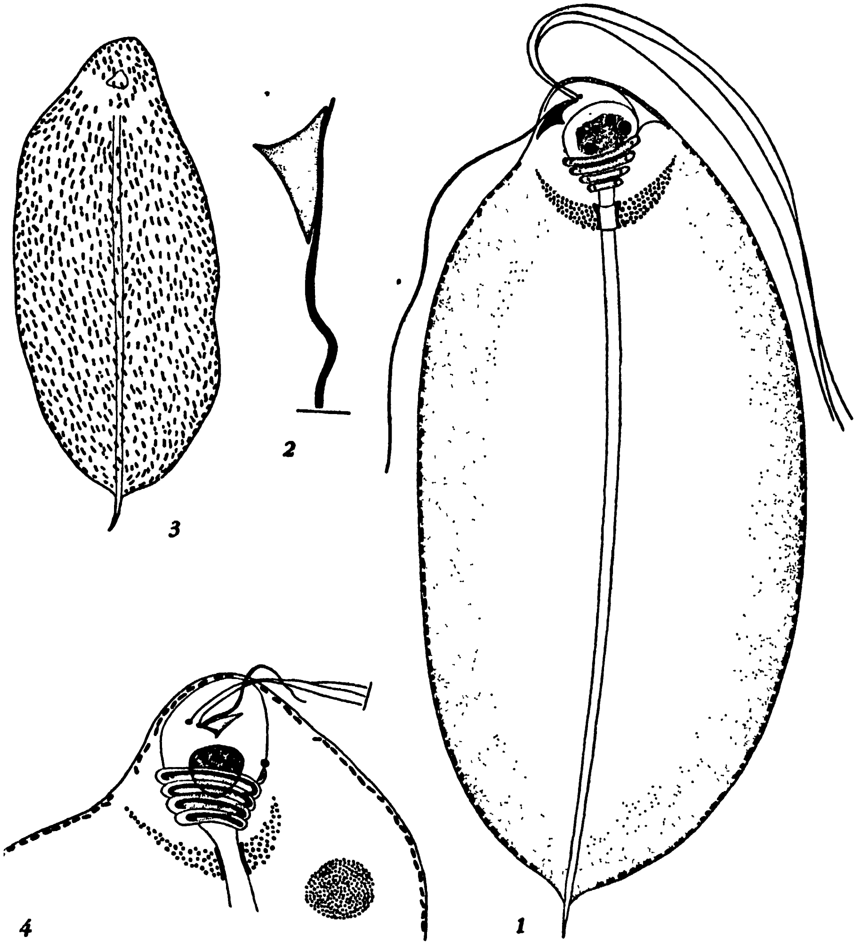

Fig. Q. *Caduceia kofoidi* sp. nov. from *Glyptotermes guianensis*. British Guiana. 1. Entire specimen. Optical section of bowl-shaped group of granules posterior to nucleus, with inner ring surrounding trunk of axostyle. Rodlets of capitular membrane and layer at periphery of body shown only at edges. × 1500. 2. Enlarged diagram of cresta and anterior part of trailing flagellum. 3. Distribution of rodlets over capitular membrane and greater part of body. 4. Detail of anterior mastigont structures, with optical section of bowl-shaped group of granules and ring. × 1800.

Whereas the rods of the cap are of similar size and evenly spaced close to one another, the rods of the body are highly variable in length and are more sparsely and unevenly arranged. Some are so short as to be merely elongate granules, others range up to $1.5\mu$ in length, and some appear to be dividing or to have divided by binary fission. The rods lie just interior to the surface layer of the body (fig. Q, 1).

Successive gyres of the parabasal body are close together, and the apparatus forms a bowl-shaped structure that fits closely against the posterior part of the nucleus (fig. Q, 1). The parabasal body is relatively more slender in *Caduceia kofoidi* than in most devescovinids. The parabasal filament may be well defined at the inner edge, and appears as a granule in optical section.

Usually the whole parabasal helix is surrounded laterally and posteriorly by a clear zone, commonly 1.5–3$\mu$ wide, that extends to the periphery of the body. No peripheral rods appear at the edges of this clear zone, and that accounts for the clear band separating the group of capitular rods from the posterior group. Though the zone is empty of all stainable or refractile material, it obviously is not an empty space, but consists of cytoplasm that provides the relationship between the structures of the anterior and posterior parts of the body.

The middle of this clear zone is crossed by the trunk of the axostyle. Fitted closely against the convex posterior edge of the clear zone, and extending a large part of the distance to the margin of the body, is a granular layer (fig. Q, 1, 4). This layer has the form of a bowl about 2$\mu$ thick in its middle part, and thinning at its upper edges. It consists of a uniform layer of evenly spaced small granules. Among these granules, in many specimens, are larger deep-staining bodies of variable size, number, and distribution.

At the place where the granular layer meets the trunk of the axostyle is a deep-staining membranous cylinder, sharply set off anteriorly and posteriorly, which surrounds the axostyle closely (fig. Q, 4). The anterior part of the cylinder may be somewhat wider and thicker than the posterior part.

The trunk of the axostyle is relatively slender, with a diameter of only about 1.5$\mu$ in the middle of the body. It tapers gradually posteriorly, and projects in a pointed end for a few microns. It appears as a simple structure, without internal membranous differentiation, as in the stouter axostyle of *Hyperdevescovina*. In its simple form it is comparable to the axostyle of other species of *Caduceia*.

The nucleus is only 3 or 4$\mu$ from the anterior edge of the body. It is almost spherical in form, but often appears somewhat larger in the transverse diameter. The chromatic material is concentrated in a central chromatic mass, with a clear zone of appreciable width around it. The chromatic mass may be somewhat irregular or angular in form. In it are rounded bodies of various sizes that stain deeply with iron-haematoxylin, and finer granular chromatin. At the periphery of the mass, wholly or partly embedded in it, is a spherical body, often about 1$\mu$ in diameter, which is stained deeply and is surrounded by a sharply defined clear zone. The clear zone is apparent not only where this nucleolus lies in the substance of the chromatic mass, but also where it extends into the outer clear zone of the nucleus, which appears a little darker.

## **Macrotrichomonas directa** sp. nov.

(Fig. R, 2; fig. S, 2)

*Type host.*—*Kalotermes* sp. El Salvador.

T-543. Mt. Cacaguatique, Dept. Morazan. (Syntype slides TP-550:2, 3, 5.)

*Diagnosis.*—Average length 45$\mu$ (range usually 34–57$\mu$, some dwarf specimens down to 21–30$\mu$); average width 18$\mu$ (range usually 15–21$\mu$, some small specimens down to 8–10$\mu$); distance between anterior end of nucleus and anterior end of body (in specimens of usual range) 12 (7–16)$\mu$; anterior flagella 20–40$\mu$ long; trailing flagellum a moderately stout cord 80–95$\mu$ long in specimens of average size; cresta 17–51$\mu$ long, 2–5$\mu$ wide near middle, anteromedial edge 4–5.5$\mu$, angle between inner edges not prominent; parabasal body turned around axostyle posterior to nucleus 2–4.5 times, averaging 3; trunk of axostyle moderately stout, sharpened posteriorly and projecting often 3–5$\mu$; nucleus ellipsoidal, elongated oblique to longitudinal axis of body, size (except in dwarf specimens) 6.3 (4.6–6.9)$\mu$ × 4.0 (2.9–4.0)$\mu$; no granules or rods on capitulum; no adherent microörganisms.

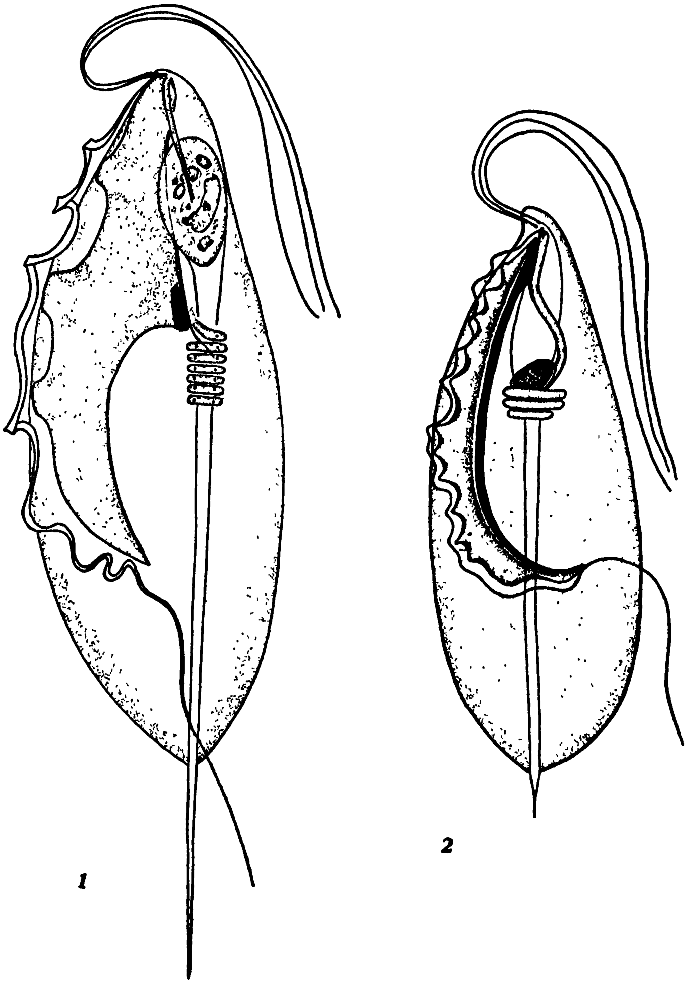

Fig. R. 1. *Macrotrichomonas emersoni* sp. nov. from *Glyptotermes hospitalis*. British Guiana. × 1250. 2. *Macrotrichomonas directa* sp. nov. from *Kalotermes* sp. nov. El Salvador. × 1500.

The blepharoplast-complex is a group of several distinctly separated granules and enlargements similar to that in *Macrotrichomonas pulchra* (Kirby, 1942, pl. 16, fig. 27).

The most distinctive feature of *M. directa* is the shape of the cresta (fig. R, 2). The anteromedial edge is relatively very short, amounting to not much more than a tenth of the total length. The angle between it and the posteromedial edge is wide and shallow, and does not stand out distinctly along the inner edge of the cresta, which appears to be much more even from anterior to posterior end than in other species; it is because of that character that the trivial name *directa* has been selected. Along the inner edge of the cresta is a rib that stains deeply by iron-haematoxylin. The edge of this rib toward the external edge of the cresta extends in an uninterrupted curve from one end of the cresta to the other. The other edge bends inward at the angle, then passes straight to the pointed anterior end of the cresta; but the increased thickness of the rib at the angle amounts to not more than 1.5 times the thickness of the rib posterior to it. If the line of the posteromedial edge were extended smoothly anteriorly, the part inward to it, at the angle, would be a very small triangle.

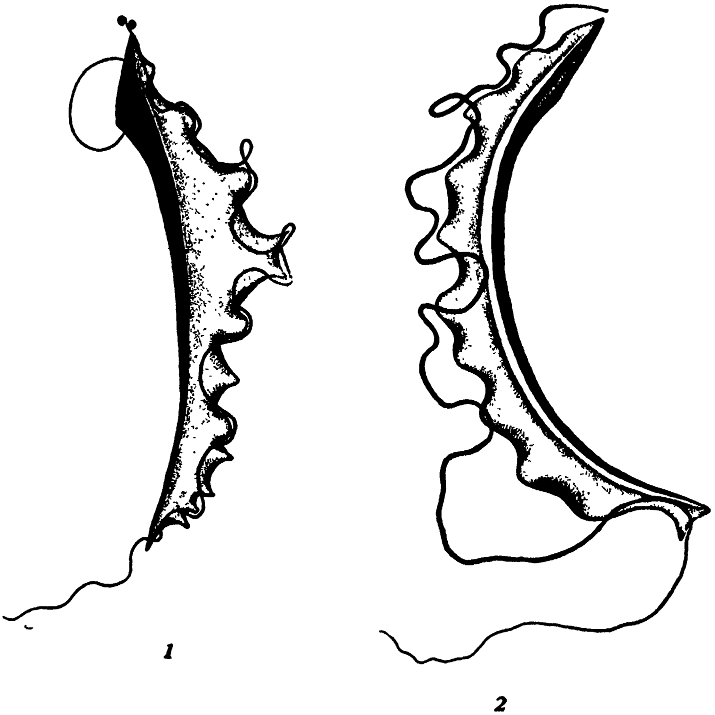

Fig. S. 1. Cresta of *Macrotrichomonas virgosa* Kirby from *Procryptotermes* T-4359, Madagascar. 2. Cresta of *Macrotrichomonas directa* sp. nov. from *Kalotermes* T-543, El Salvador. Diagrams for comparison. Cresta of *M. directa* narrower, with wider angle at meeting of the two inner edges. × 1800.

The rib of the cresta has sharply defined margins, and is paralleled in the interior of the cresta by a clear zone (fig. S, 2). Exterior to this clear zone is the gray-staining membranous part of the cresta, which is undulated at its outer part. The outermost border of the cresta often stains or impregnates more deeply than the part adjacent to it, so that it appears as a filament; but this may not be visible when the cresta is observed on its broad surface.

A filament parallels the anteromedial edge of the cresta and extends for 2 or 3μ posterior to the angle; this posterior part is turned away from the cresta. The filament was impregnated consistently and appeared black and rather stout in the protargol preparations that I examined; it was not stained so regularly in Heidenhain preparations. A constant and notable feature of the structure is a short protuberance along the first part of the posteromedial edge of the cresta, which gives the structure much the shape of a boathook. It is not possible to be certain from the position of this structure that it does not actually belong to the substance of the cresta, but its chemical reactions are different. The adjacent parts of the cresta do not impregnate so deeply with protargol. The filament evidently corresponds to the paracrestal or accessory filament of *Macrotrichomonas pulchra;* but it is much shorter than the filament in that devescovinid, and it stops far short of the coiled part of the parabasal body.

The parabasal body (fig. R, 2) begins at the level of the anterior end of the cresta, passes along the anteromedial edge of the cresta close to the accessory filament, then follows the posterior part of this filament in turning away from the cresta. In continuing toward the nucleus, it follows a wide helical turn, crosses the nucleus at its anterior part or middle, then turns around the trunk of the axostyle in a counterclockwise spiral. The parabasal body has the same thickness for all its length; no enlargement and no bend occur at its anterior end.

The use of the published key to the species of *Macrotrichomonas* (Kirby, 1942, p. 115) for this flagellate would lead to *M. virgosa;* but, in other characteristics than those given in the key, there are marked differences between the two species. The anteromedial edge of the cresta is also relatively short in *M. virgosa,* though it measures a few microns longer. In that species the cresta (fig. S, 1) is usually larger, and its width averages nearly twice that of the cresta of *M. directa.* The nucleus of *M. virgosa* is more anterior in position, and the inner angle of the cresta is near it, whereas in *M. directa* the nucleus is posterior to this angle by some distance. The more posterior position of the nucleus in *M. directa* results in a relatively long anterior part of the parabasal body. In *M. virgosa* the axostyle has a much longer posterior projection, the trailing flagellum is somewhat more slender, and there are many adherent rods and spirochaetes.

### **Macrotrichomonas emersoni** sp. nov.

(Fig. R, 1; fig. T, 1–5)

*Type host.*—*Glyptotermes hospitalis* Emerson.

Kartabo, British Guiana. (Syntype slides TP-586:3, 4.)

*Diagnosis.*—Length 79 (60–90)μ; width 29 (23–36)μ; three long anterior flagella; trailing flagellum band-formed, 1.5–2μ wide, much longer than body; cresta large, anteromedial edge 25–29μ long, posteromedial edge 27–29μ long; greatest breadth 12–15μ, concave, shelf-like, more or less rectangular extension or unguis present, size about 2.5 × 5μ, at posterior

**part of anteromedial edge; accessory filament extending along, and short distance posterior to, anteromedial edge, free filament enclosed within coil of parabasal body; parabasal body coiled closely in 3–12 gyres, mode 5, seldom more than 7 gyres; capitulum of axostyle bordered ventrally by suspensorial lamella; trunk of axostyle projecting posteriorly 9–40μ, averaging 23μ; distance from anterior end to nucleus 5–8μ; nucleus ellipsoidal, longitudinal, 10–15μ × 7–8μ; no spirochaetes adherent to posterior part of body; small group of spirochaetes, many about 10μ long, adherent to anterior end of body near origin of flagella.**

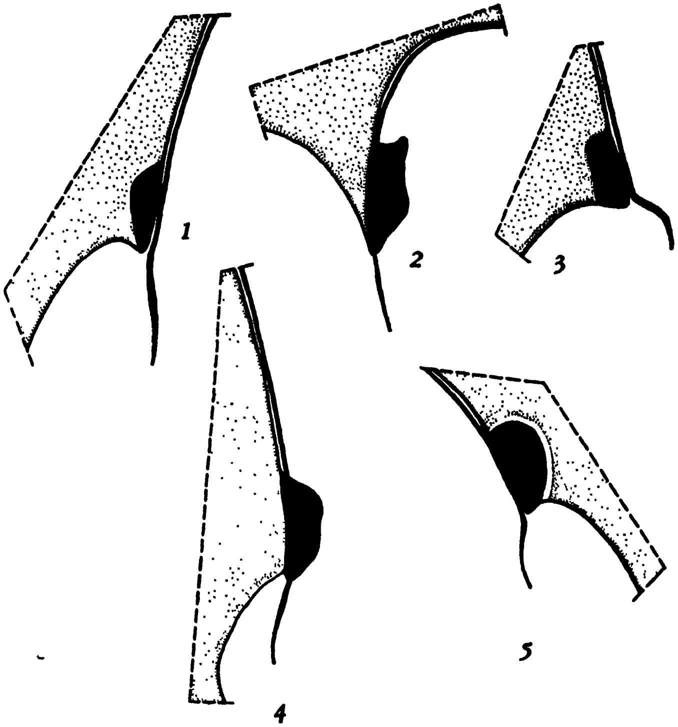

Fig. T. *Macrotrichomonas emersoni.* × 2200. Detail of inner angle of cresta between anteromedial and posteromedial edges. Shelf-like unguis at posterior part of anteromedial edge. In 4 and 5 this is shown projecting from edge. In the others it overlaps rest of cresta. It stains deeply with iron-haematoxylin. Paralleling anteromedial edge and extended posteriorly inside coil of parabasal body is paracrestal or accessory filament.

The cresta of this species (fig. R, 1) is much like that of *M. unguis*. It is similar in size and form, and also has the membrane extended from the posterior part of the anteromedial edge, which was called the "unguis" in that species. The membrane (fig. T) has a more or less quadrangular form and is turned at an angle to the cresta, so that from one aspect it appears to lie over it. The membrane stains deeply at the same time that parts of the cresta near by may have a lighter stain, so that when lying over the cresta it may suggest a deep-stained thickening at the inner angle. An accessory filament (fig. T, 1, 3) borders the anteromedial edge of the cresta and extends posteriorly, as a rather stout filament, for a short distance beyond the angle. This projecting filament passes within the anterior part of the coil of the parabasal body, applied to the axostyle, which it crosses at an angle. It can often be followed clearly beyond the inner angle of the cresta for a distance of 4 or 5μ.

The longitudinal part of the parabasal body extends the whole length of the anteromedial edge of the cresta; just posterior to the angle it turns in a close spiral. A deep-staining filament is present at its inner edge.

The capitulum of the axostyle is moderately expanded; along its edge, from the region of the flagellar granules to the nucleus, is a band that tapers posteriorly (fig. R, 1). This band resembles the structure in *M. pulchra* that was called the suspensorial lamella.

A distinctive feature of the species is the long, slender posterior projection of the trunk of the axostyle. In many specimens on the slides, the projection is broken off, and a truncate stump may be seen. There is no doubt, however, of the normal presence of this long projection, which suggests that which is seen in some species of *Hyperdevescovina.*

*M. emersoni* has some points of resemblance to *M. pulchra,* but differs notably in that the cresta is much larger and possesses the unguis. The resemblance to *M. unguis* is greater than the resemblance to *M. pulchra.* The most marked difference from *M. unguis* is in the projection of the axostyle. In the flagellate of *Glyptotermes* sp. from Java and Ceylon, the axostyle does not project more than a few microns, in contrast to the long projection characteristic of *M. emersoni.* In the specimens of the two species that I have examined, the nucleus of *M. emersoni* is much larger.

### **Macrotrichomonas procera** Kirby

*Additional hosts.*—
*Caloaritermes* sp. nov. El Salvador.
T-545. Volcan de Santa Ana, Dept. Santa Ana. (Homosyntype slide TP-552:12.)
*Calcaritermes* sp. nov. El Salvador.
(Emerson *in litt.* possibly new subspecies of T-545, or different species.)
T-548. Chilate, Dept. Sonsonate. (Homosyntype slide TP-555:10.)

The specimens resemble the type in every respect, including the assemblage of spirochaetes adherent to the posterior part of the body. In heavily stained specimens from T-545 I observed a band shaped like a napkin ring, around the posterior part of the axostyle just before it projects from the body; this structure was not recorded in the original description of the species.

*Macrotrichomonas procera,* which has been found in every other species of *Calcaritermes* examined, was not present in a series of preparations from *Calcaritermes nigriceps.*

## FURTHER DISCUSSION OF DEVESCOVINA ELONGATA BERNSTEIN

The following additions to the synonymy given by Kirby (1941) are necessary.

**Devescovina elongata** Bernstein

*Polymastix lineatus* Duboscq, Grassé & Rose. Duboscq & Grassé, 1943, Arch. Zool. exp. gén., 82:405, fig. II.

? *Strobilonympha schizophyla* De Mello & Monteiro, 1942, Arqu. Esc. méd.-cirurg. Nova Goa (A), fasc. 18:1, pl. 3, fig. 1.

? *Strobilonympha pisciformis* De Mello & Monteiro, 1942, Arqu. Esc. méd.-cirurg. Nova Goa (A), fasc. 18:1, pl. 3, fig. 2.

? *Strobilonympha serpentiformis* De Mello & Monteiro, 1942, Arqu. Esc. méd.-cirurg. Nova Goa (A), fasc. 18:2, pl. 3, fig. 3.

When Duboscq, Grassé and Rose referred to this flagellate in *Anacanthotermes ochraceus* as *Polymastix lineata,* they remarked about its resemblance to *Devescovina elongata,* but considered that neither it nor Bernstein's flagellate belonged in the genus *Devescovina.* It differed from *Polymastix,* they stated, only in size and in the greater development of the parabasal body. A resemblance to *Polymastix* was suggested by the two anterior granules shown by Bernstein, and the similarity of the adherent rods to those on species of that genus, especially *P. legeri.* It was shown by Kirby (1941), however, that the blepharoplast grouping is like that in *Devescovina;* and the nature of adherent microörganisms does not constitute a generic characteristic.

Duboscq and Grassé (1943) gave an illustrated description of the flagellate, which they then named *Polymastix lineatus.* They referred to the statement by Kirby (1937, p. 203) that a flagellate similar to *Devescovina elongata* Bernstein is present in *Anacanthotermes ochraceus,* and that it has a cresta and trailing flagellum. They had not had access to the illustrated account by Kirby (1941), but rejected the claim of the presence of a cresta and trailing flagellum.

They encountered larger specimens than Kirby had had in his preparations, and found that the flagellate may attain a length of $108\mu$. They found a group of anterior flagella, numbering two, three, or four, formed in a whip and, as shown in their figure II, A, originating in the same manner as in a devescovinid or other trichomonad flagellate. They stated that they saw the axostyle, which is represented in one figure. It is unlike the short filament in *Polymastix* that Grassé (1926, p. 458) had suggested might be a parabasal body. They showed also a devescovinid type of parabasal body, as had been represented by Bernstein and Kirby. But no such structure has been found in *Polymastix,* unless it is a homologue of the filament; if so, the axostyle is without an equivalent structure in *Polymastix.* They state that the flagellate is related to *Polymastix* because of the absence of a rostrum, the manner of implantation of the flagella, the elongate form, and the manner of fixation of bacteria. But actually none of the four features is significant in the diagnosis of a genus. In the first two features the resemblance of the flagellate is to

***Devescovina*** rather than to ***Polymastix,*** as the figures by Kirby (1941) show. Although *D. elongata* has the most elongated body form in the genus, some other species—for instance, *D. exilis*—have forms not greatly unlike it; furthermore, the aciculate shape does not more closely resemble that typical of *Polymastix.* It should not be forgotten, in the last matter, that all species of *Devescovina* have longitudinally adherent rod-shaped microörganisms. The existence of a cresta and trailing flagellum cannot be doubted, and the flagellate certainly is a devescovinid. It is true that it has certain features not typical of *Devescovina,* but it is more like that genus than any other. It seems better to place it there than to attempt to define a new genus on the basis of a minor difference in the shape of the anterior end and a different type of rod on the surface.

De Mello and Monteiro (1942) described three species of *Strobilonympha* in *Anacanthotermes viarum* from Coimbatore, India. *Strobilonympha* is considered by them to be a hypermastigote covered with flagella; they stated that it is related to *Teratonympha.* I am convinced, however, from observation of their figures, that what they actually studied is a flagellate of the same sort as *D. elongata,* and that possibly it is the same species. *Anacanthotermes viarum* harbors a species of *Trichonympha* that is probably the same as that in *A. ochraceus.* The flagellate faunules of the two hosts are related if not identical.

My reasons for believing that *Strobilonympha* is a devescovinid flagellate are these. The shape and size of the body correspond in general to those of *D. elongata,* and the same kinds of axostyle and parabasal body are present. The spirochaetes and longitudinal rods on the surface are similar to those on *D. elongata.* I know of no other polymastigote or hypermastigote flagellate in which the same combination of characteristics could have been observed. The detail shown for nuclear structure and division with a paradesmose also corresponds to what occurs in devescovinid flagellates.

To establish the suggested relationship to the flagellate of *A. ochraceus,* one has only to suggest some additions to De Mello and Monteiro's observations and some changes in their interpretations. The flagella, three anterior and one recurrent, together with the small cresta, may possibly have been overlooked. The longitudinal "scales or spikes," the arrangement of which suggested pseudometamerism to the authors, are the adherent microörganisms. The dense, fine coat of cilia over the whole body is apparently an artifact, owing perhaps to the nature of the preparation. The size differences, and the number of adherent spirochaetes, which led the authors to differentiate *Strobilonympha schizophyla* and *S. pisciformis,* are possibly within the range of variation of a species. *S. serpentiformis* is unlike any known flagellate, and has a structure that is highly improbable. It seems possible that parts of two separate flagellates were combined in the supposed organization of that species.

## SUMMARY

A description is given of the genus *Hyperdevescovina,* which was named and briefly characterized by Kirby, 1947.

The genus differs from others in having a particular sort of cresta, with two equal sides diverging from the apex near the blepharoplast, and a concave posterior margin. It has three anterior flagella, and the recurrent flagellum is moderately developed and usually shorter than the body. The trunk of the axostyle projects posteriorly, without posterior enlargement, for a distance that is short in some species, long in others. The capitulum of the axostyle is often extended in a pennant-shaped or cape-formed membrane, over which rods are usually present. Most species have rodlets in a narrow or wide belt in the peripheral cytoplasm of the middle or posterior part of the body.

Eight species of *Hyperdevescovina* are described, seven of which are new: *H. calotermitis* (Nurse), *H. caudata* sp. nov., *H. mitrata* sp. nov., *H. riciniata* sp. nov., *H. insignita* sp. nov., *H. balteata* sp. nov., *H. falcifera* sp. nov., and *H. torquata* sp. nov.

The species of *Hyperdevescovina* occur in eight termites of the Australian Region, one termite of South Africa, and one of Ceylon. All except the Ceylon host belong to an interrelated group for which Emerson (MS) proposes the new genus name *Proglyptotermes*. The generitype is *P. hilli* Emerson, a new name for *Kalotermes obscurus* Walker. The other species in the Australian Region are *P. brouni* (Froggatt), *P. pallidinotum* (Hill), *P. tillyardi* (Hill), *P. atratus* (Hill), *P. spoliator* (Hill), *P. rufinotum* (Hill), and *P. banksiae* (Hill). All the new combinations are by Emerson.

Not more than one species of *Hyperdevescovina* is present in a host. There are two pairs of hosts in Australia in which the same species occur, but otherwise each host termite has a different flagellate of the genus.

The new species belonging to genera previously considered in this monograph are *Foaina inflata* sp. nov., *F. serrata* sp. nov., *Devescovina cuneata* sp. nov., *D. minor* sp. nov., *Caduceia kofoidi* sp. nov., *Macrotrichomonas directa* sp. nov., and *M. emersoni* sp. nov.

*Foaina inflata* is of particular interest because of the inflated form of the parabasal body, an inflation that occurs also, though in a different manner, in the parabasal body of *Bullanympha silvestrii. Foaina serrata* has a prominent filament that borders the parabasal body and extends beyond it; this structure throws light on the nature of filaments that have been described along the cresta and parabasal body of various devescovinids. *Caduceia kofoidi* shows a feature of special interest in a bowl-shaped, transverse mass of granules a short distance posterior to the parabasal body.

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# PLATES

All figures have been drawn with the aid of the camera lucida.

Abbreviations for methods of preparation: B., Bouin's fluid; C., Champy's fluid; D., Delafield's haematoxylin; Ehr., Ehrlich's haematoxylin; Fl., Flemming's fluid; H., Heidenhain's iron-haematoxylin; Prot., protargol; R., Regaud's haematoxylin.

## PLATE 45

*Hyperdevescovina calotermitis* (Nurse) from *Proglyptotermes brouni*

Fig. 1. Entire specimen, but flagella shown only in their basal part, and adherent spirochaetes are omitted. Distribution of wood and granules in the cytoplasm is shown. Slender, slightly curved rods adherent to posterior part of body. S.H. × 1335.

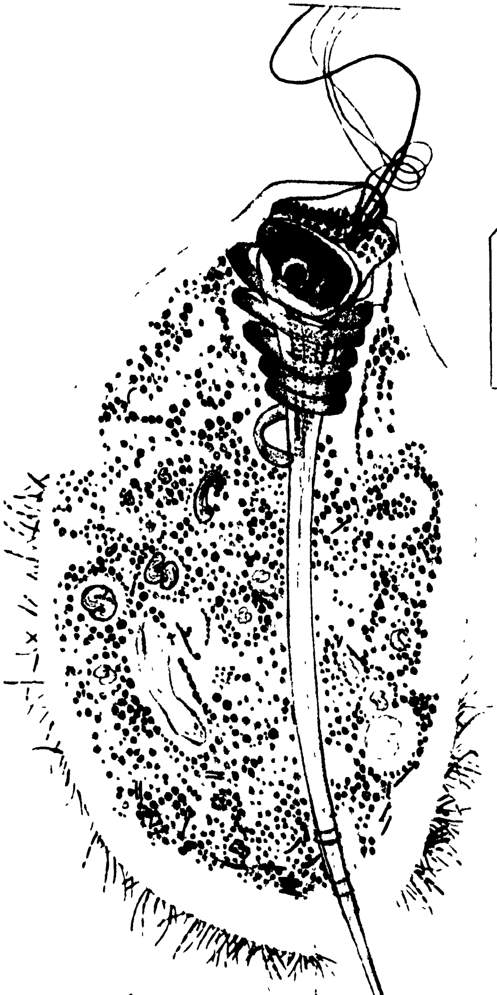
Fig. 2. Anterior part of mastigont; capitulum of axostyle; cresta; filament leading to parabasal body; granules on capitulum. S.H. × 2335.

Fig. 3. Triangular membrane of capitulum; its relation to parabasal body; granules of capitulum. S.H. × 2335.

Fig. 4. Cresta; transverse band of capitulum; the two roots of the anterior flagella; trailing flagellum; band-shaped nuclear rhizoplast (on right); accessory filament, exceptionally broad bands; curved rod above cresta, which is attached to proximal part of accessory filament. S.H. × 2335.

Fig. 5. Structures as in fig. 4, but nuclear rhizoplast not shown. Extending posteriorly from blepharoplast-complex is elongated, angular mass of stainable substance, which appears as a more slender mass in fig. 4. S.H. × 2335.

Fig. 6. Sigmoid curvature of accessory filament; attachment of curved rod above cresta to proximal part of that structure. S.H. × 2335.



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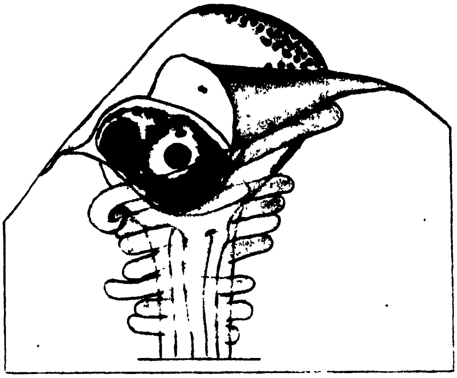

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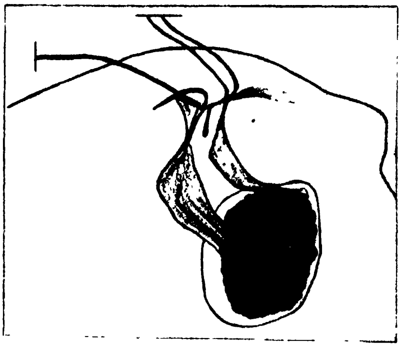

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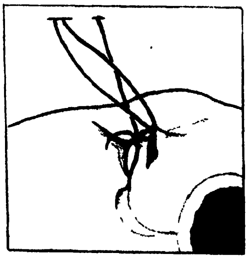

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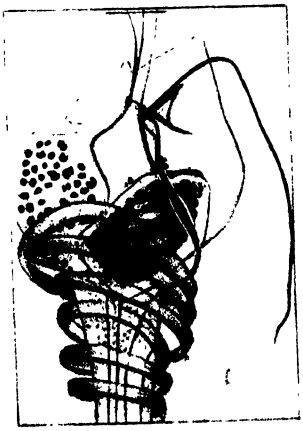

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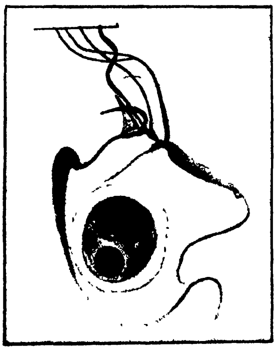

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# PLATE 46

*Hyperdevescovina calotermitis* (Nurse) from *Proglyptotermes brouni*

Fig. 7. Accessory filament somewhat sickle-shaped, heavily stained; passes along edge of proximal part of parabasal body. Nuclear rhizoplast appears as a filament. S.H. × 2335.

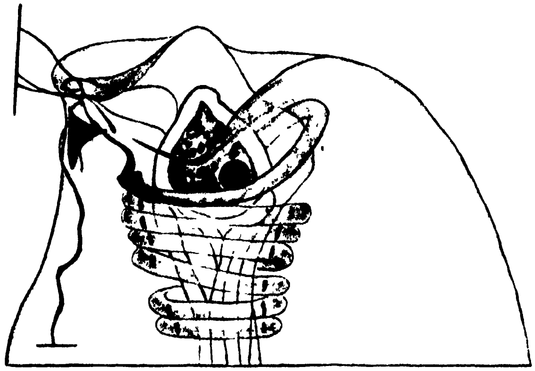
Fig. 8. Nuclear rhizoplast and accessory filament both band-formed. S.H. × 2335.

Fig. 9. First gyre of parabasal body separate from and wider than rest of spiral. Small granules abundant in anterior part of trunk of axostyle. S.D. × 2335.

Fig. 10. Capitulum and anterior part of trunk of axostyle; triangular membrane of capitulum; position of nucleus in relation to axostyle. S.H. × 2335.

Fig. 11. Parabasal body and its relation to capitulum and trunk of axostyle. S.H. × 2335.

Fig. 12. Core of axostyle continues to posterior end of nucleus, near which it contains a number of granules and is covered in anterior part by a sheath. Outside of this is a broad expansion on dorsal side, in which is a band parallel to outermost membrane. S.H. × 2335.



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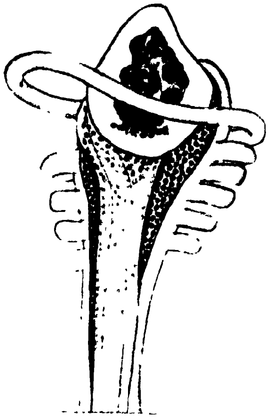

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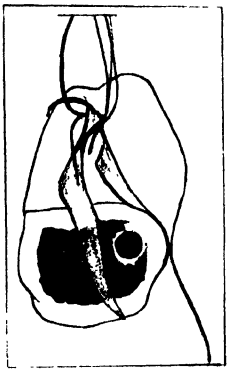

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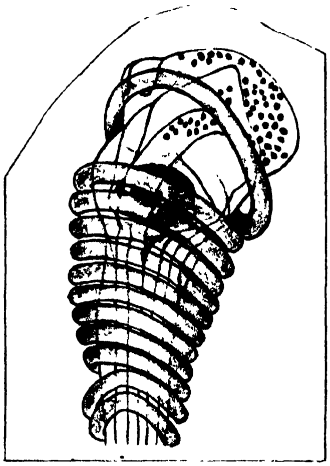

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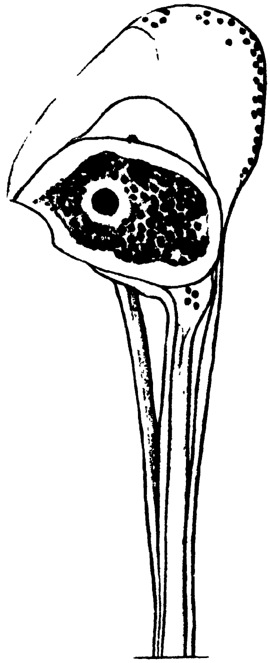

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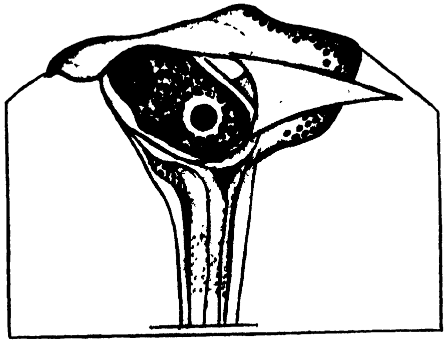

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# PLATE 47

*Hyperdevescovina calotermitis* (Nurse) from *Proglyptotermes brouni*

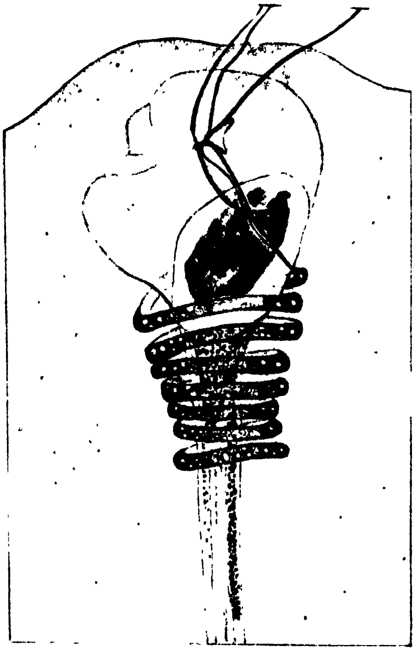
Fig. 13. Parabasal body stained by Delafield's haematoxylin after fixation in Schaudinn's fluid with acetic acid. Accessory filament between anterior part of parabasal body and blepharoplast-complex. Small granules present inside trunk of axostyle. S.D. × 2335.

Fig. 14. First gyre of parabasal body passes around capitulum. In core of axostyle is triangular group of granules just posterior to nucleus. Stained parabasal filament (here a band) visible at inner margin in parabasal turns. Several membranes of axostyle can be followed forward into capitulum, in which are numerous granules. S.H. × 2335.

Fig. 15. Parabasal body is drawn out and wound tightly around trunk of axostyle for most of its length. S.D. × 1150.

Figs. 16–18. Spiral filament around trunk of axostyle near posterior end of body. S.H. × 1335.

Fig. 19. Parabasal body is interrupted in drawing, where it lies over axostyle, in order to show clearly the layer of small granules that lies within trunk of axostyle in its proximal part. S.H. × 2335.



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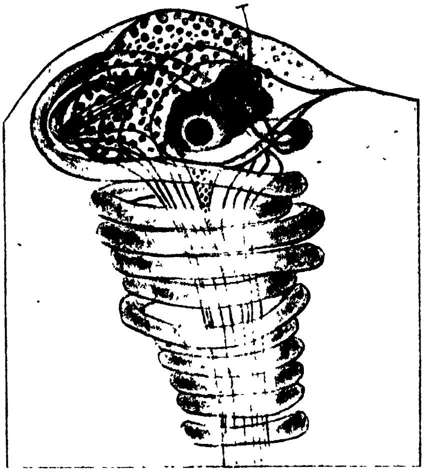

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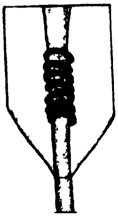

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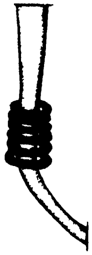

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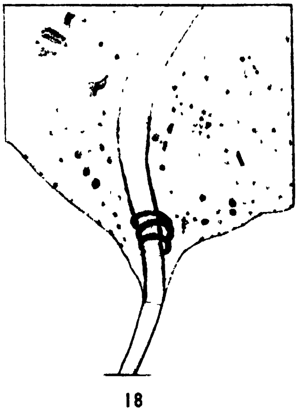

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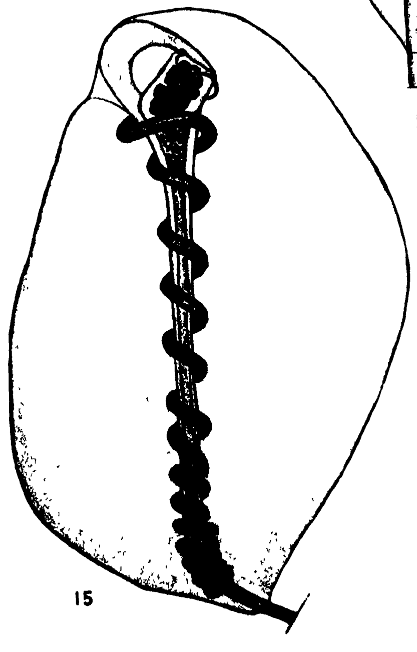

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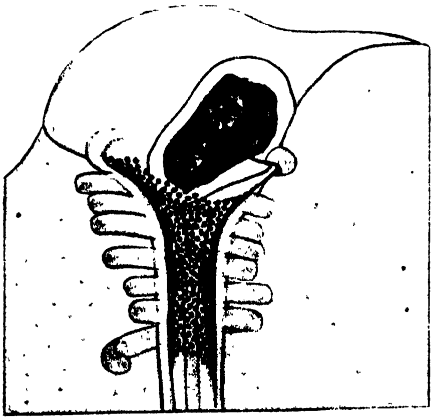

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## PLATE 48

*Hyperdevescovina calotermitis* (Nurse) from *Proglyptotermes brouni*

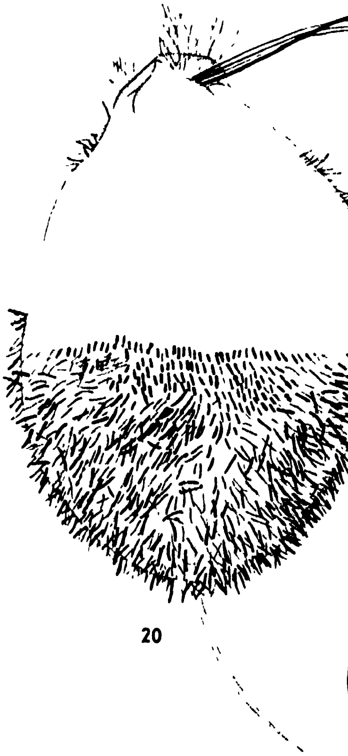
Fig. 20. Adherent organisms and band of peripheral rods. Anteriorly, group of spirochaetes adherent to surface over capitulum. Band of short, stout peripheral rods at anterior end of posterior group of adherent microörganisms. Posterior to band are abundant curved rods; this zone extends farther forward on other side of body, so that some are shown at edges. S.H. × 1150.

Fig. 21. Body distorted. Anterior group of spirochaetes as seen from top. Band of peripheral rods marks border of a region with more slender, curved rods interspersed with spirochaetes like those of anterior group. Other side of posterior part of body completely covered with these microörganisms. S.H. × 1150.

Fig. 22. Spherules, which are present in many specimens and abundant in some. S.H. × 1150.

Fig. 23. Wood particles confined to region around trunk of axostyle. Rods present among wood particles also confined to this region. S.H. × 1150.

Fig. 24. Rods, which are constantly present in cytoplasm among wood particles, shown by themselves. Wood particles omitted in drawing. S.H. × 1150.



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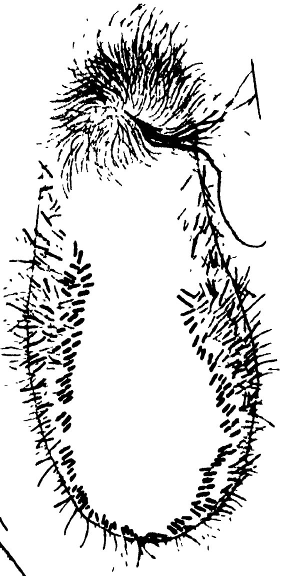

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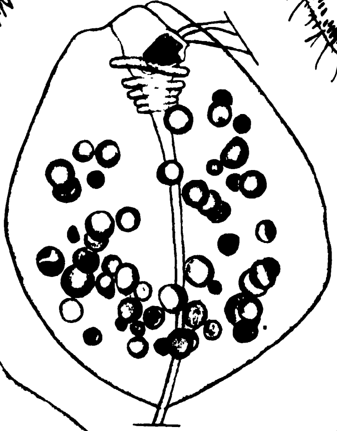

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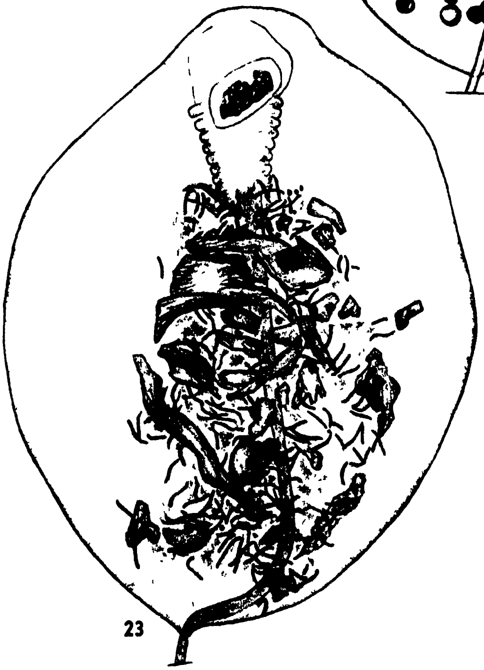

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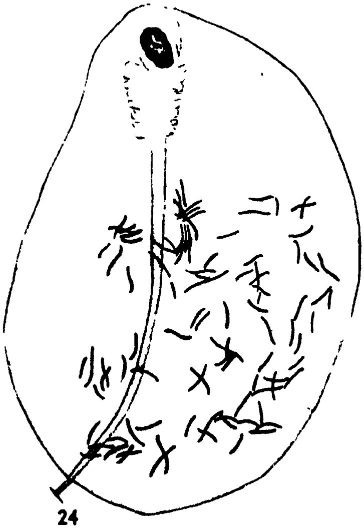

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## PLATE 49

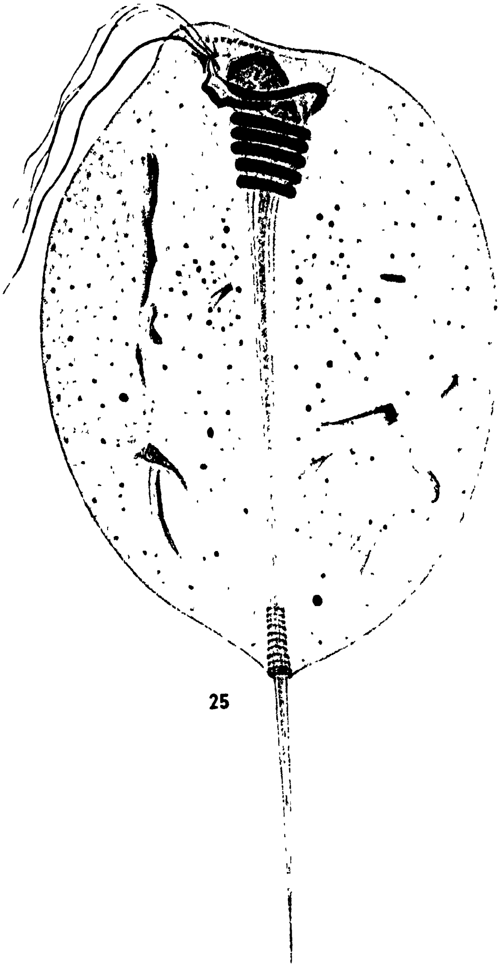
### *Hyperdevescovina caudata* sp. nov. from *Proglyptotermes* sp. nov. South Africa

Fig. 25. Entire specimen, but adherent microörganisms and peripheral rodlets omitted. Accessory filament not applied closely to parabasal body. Fl.R. × 1400.

Fig. 26. Peripheral rodlets over capitulum; parabasal body with band at inner margin corresponding to parabasal filament. See fig. 29 for drawing of same specimen emphasizing other structures. S.H. × 2400.

Fig. 27. Parabasal body, small vacuoles in substance. S.D. × 2400.

Fig. 28. Adherent microörganisms and belt of peripheral rods around body. S.H. × 1165.



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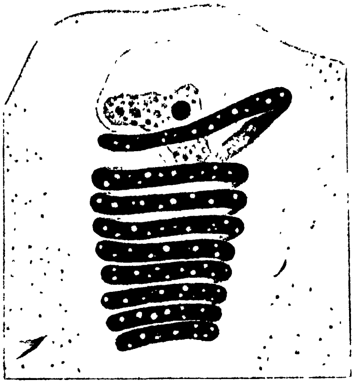

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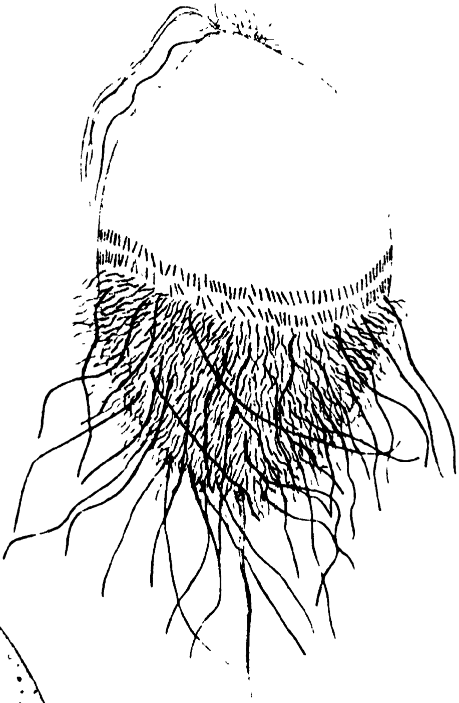

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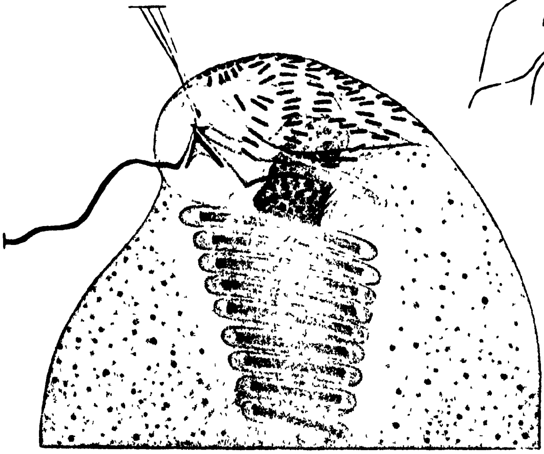

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## PLATE 50

*Hyperdevescovina caudata* sp. nov. from *Proglyptotermes* sp. nov. South Africa

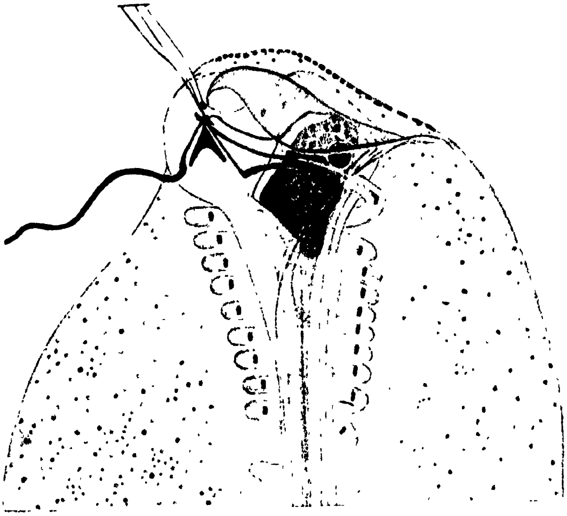
Fig. 29. Drawing of same specimen as in fig. 26. Capitulum; rods over capitulum as seen in optical section at edge of body; cresta and the two bodies giving origin to flagella; parabasal filament or band as seen in optical section at inner edge of parabasal body. S.H. × 2400.

Fig. 30. Complex fibrillar appearance of anterior part of trunk of axostyle and posterior part of capitulum. S.H. × 2400.

Fig. 31. Diagram showing cresta and flagella, the two bodies at the inner ends of flagella and connection between them, rod extending posteriorly from blepharoplast, and accessory filament paralleling, but not in contact with, part of parabasal body. S.H. ×2400.

Fig. 32. Sleeve and spiral filament surrounding trunk of axostyle in posterior part of cytosome. S.H. × 2400.

Fig. 33. Small and large adherent spirochaetes covering posterior part of body; group of small spirochaetes adherent to region above capitulum. S.H. × 670.



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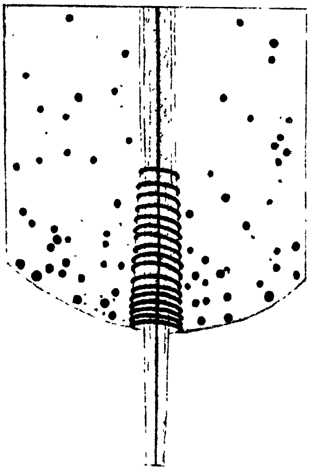

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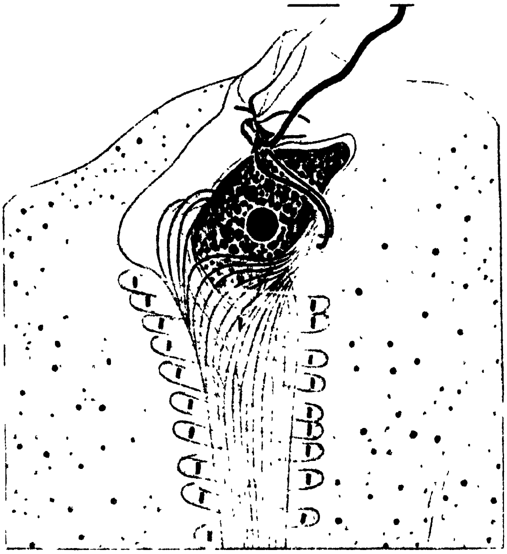

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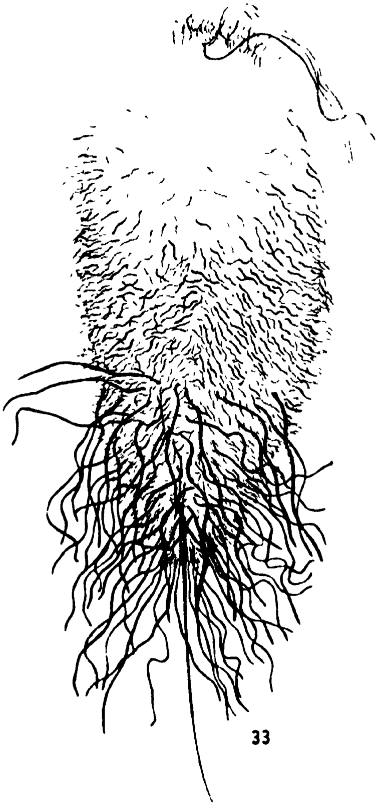

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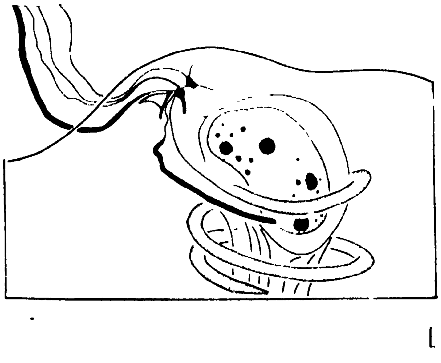

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## PLATE 51

*Hyperdevescovina mitrata* sp. nov. from *Proglyptotermes pallidinotum*

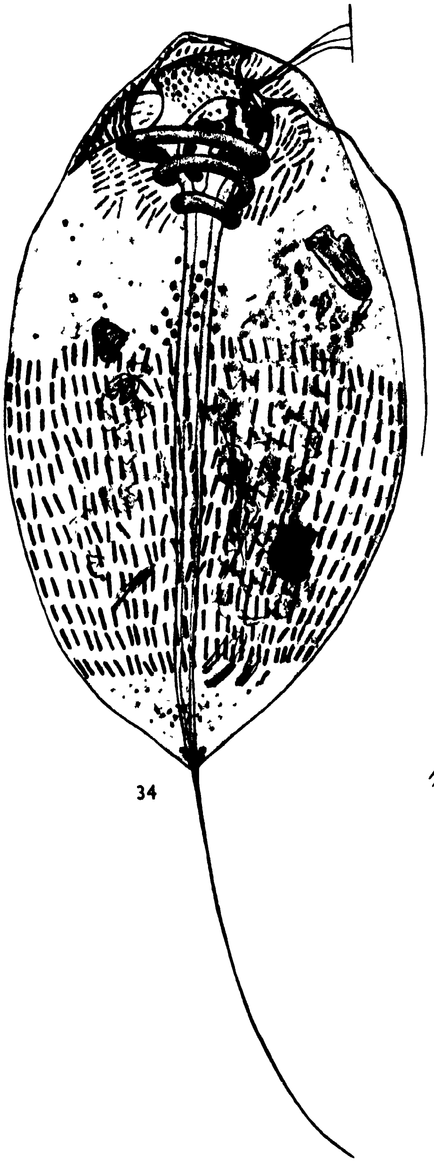
Fig. 34. Entire specimen, with rods over capitular membrane and under membrane of posterior part of body. Externally adherent microörganisms omitted. S.H. × 1700.

Fig. 35. Distribution of rods over capitular membrane. Granules between membrane and body surface anteriorly are optical sections of rods in this region. S.H. × 1535.

Fig. 36. Cresta, origin of three anterior flagella and trailing flagellum, accessory filament passing along anteromedial edge of cresta, parabasal filament paralleling accessory filament, nuclear rhizoplast passing to nuclear membrane. Between proximal ends of nuclear rhizoplast and parabasal filament is a rounded, stained body. S.H. × 2335.

Fig. 37. Spirochaetes adherent to posterior part of body, posterior to zone of peripheral rods. S.D. × 2335.

Fig. 38. Spindle-shaped microörganisms adherent to posterior part of body. Spirochaetes among which these are present are not shown. S.D. × 2335.



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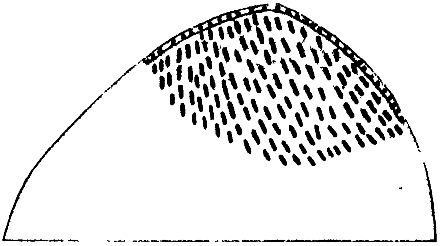

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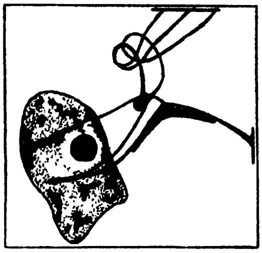

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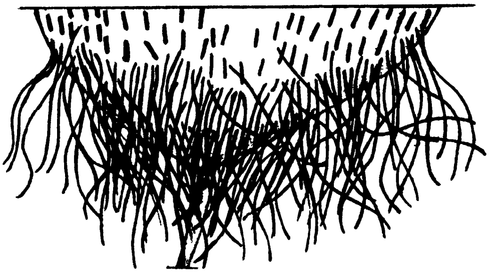

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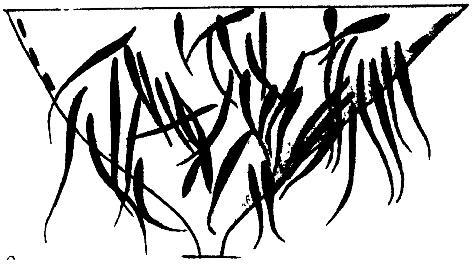

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## PLATE 52

Figs. 39–40. *Hyperdevescovina mitrata* sp. nov. from
*Proglyptotermes tillyardi*

Fig. 39. Rods above capitular extension, appearing as granules in optical section; rods on main part of capitulum, beside and anterior to nucleus; rods of same type in cytoplasm. S.H. × 1535.

Fig. 40. Capitular membrane rods as seen in optical section, larger rods showing variability in shape and size. S.H. × 1895.

Figs. 41–45. *Hyperdevescovina riciniata* sp. nov. from
*Proglyptotermes atratus*

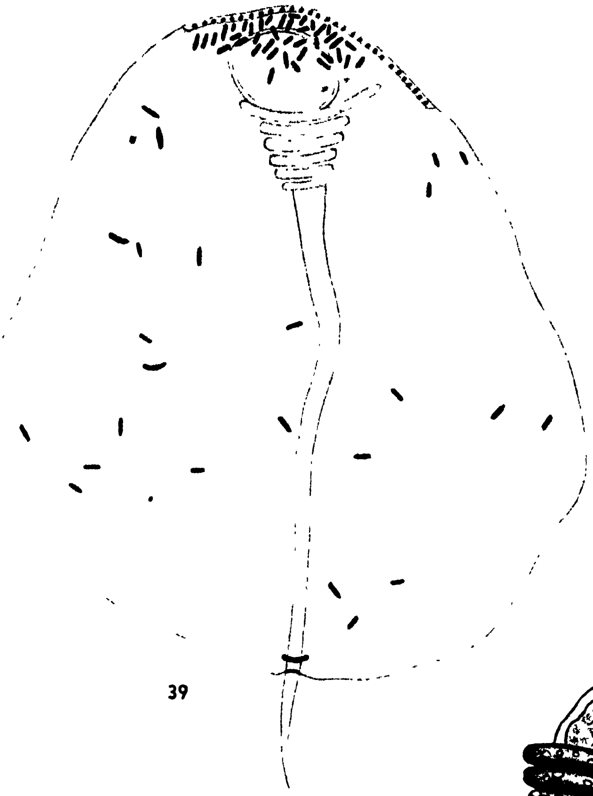
Fig. 41. Main part of capitulum; nucleus; scimiter-shaped membranous extension of capitulum. S.H. × 2335.

Fig. 42. Cresta; accessory filament; parabasal filament; nucleus; coiled parabasal body without ramus. S.D. × 2335.

Fig. 43. Similar. Parabasal body with a ramus in posterior part. S.D. × 2335.

Fig. 44. Parabasal body with a ramus in posterior part and a gap in main substance crossed by a filament. S.D. × 2335.

Fig. 45. Parabasal body with a ramus turned away from the helix, instead of parallel to it as in others shown. S.D. ×2335.



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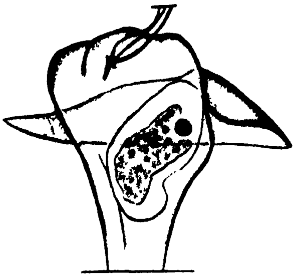

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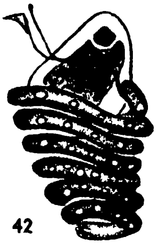

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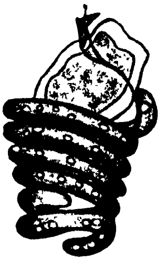

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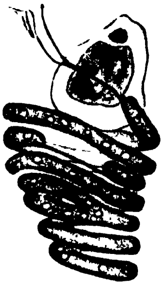

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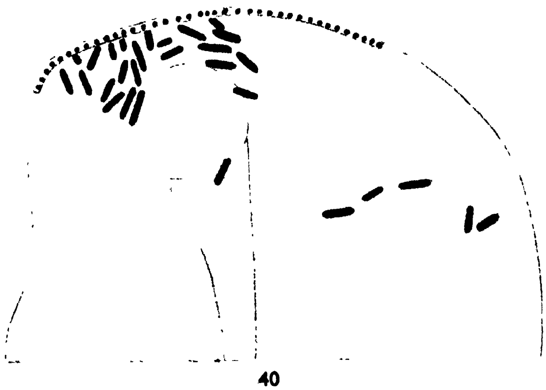

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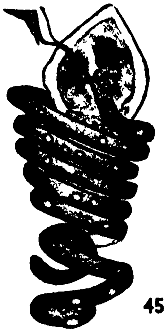

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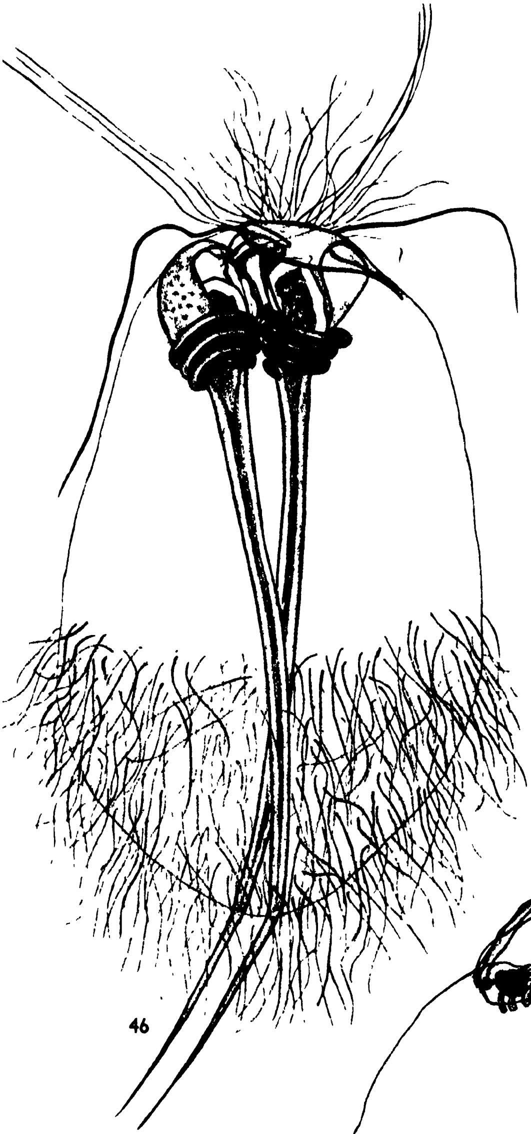
## PLATE 53

*Hyperdevescovina riciniata* sp. nov. from *Proglyptotermes atratus*

Fig. 46. Double animal with two completely reorganized mastigonts; adherent spirochaetes. S.H. × 1700.

Fig. 47. Capitulum and flap turned back from right margin; anterior plexus in which mastigont structures originate, including three granule-like enlargements in a row, a curved rod passing anteriorly from granule nearest cresta, accessory filament passing posteriorly from same granule. Parabasal body has deep-stained, band-formed filament at inner edge of helix. S.H. × 2335.

Fig. 48. Seven completely reorganized mastigonts in one cytoplasmic body. S.H. × 600.



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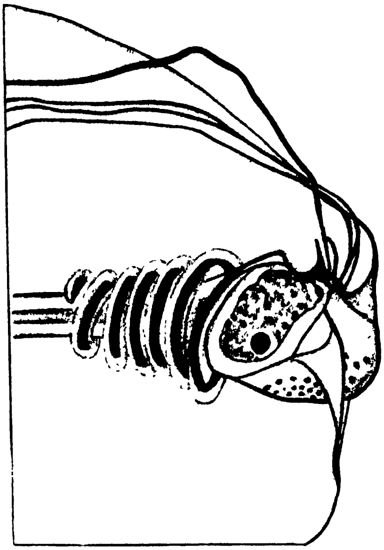

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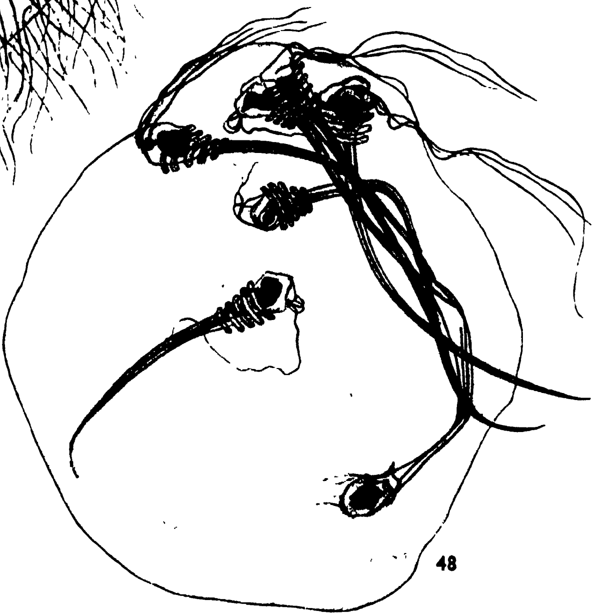

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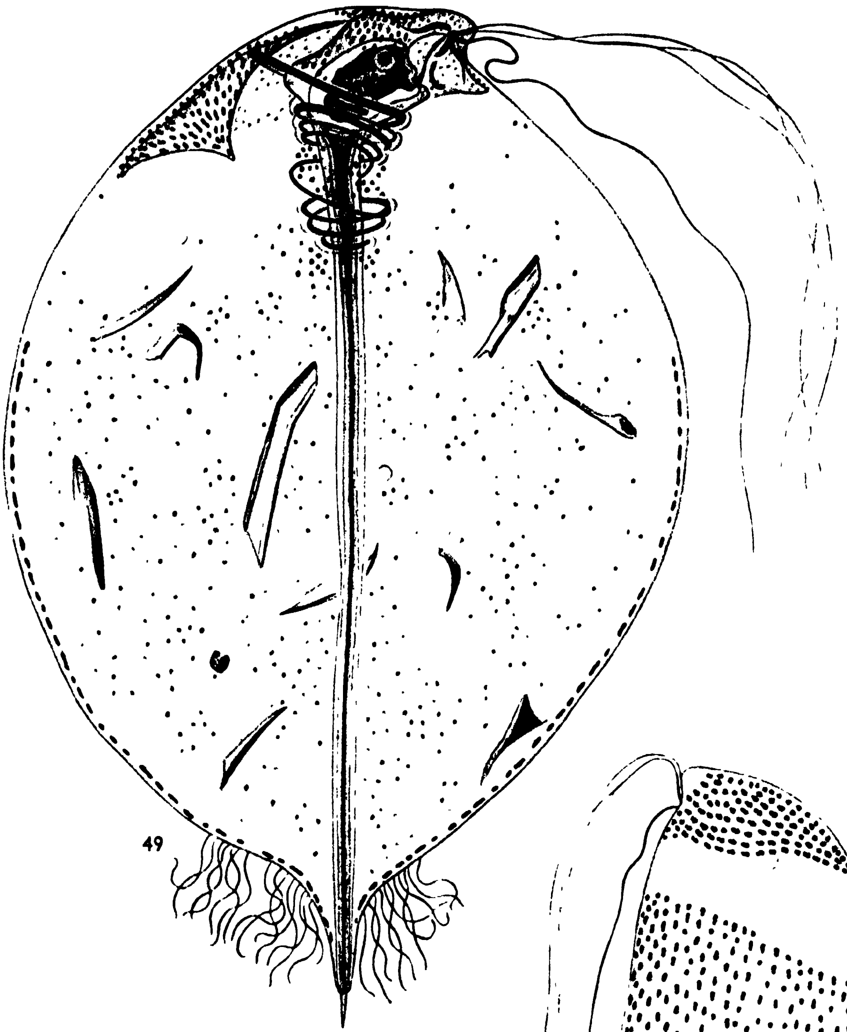
## PLATE 54

*Hyperdevescovina insignita* sp. nov. from *Neotermes militaris*

Fig. 49. Entire specimen, with adherent spirochaetes; complete capitular expansion, with covering rodlets. Parabasal body has a ramus that branches off at second gyre, but rejoins main part at fourth gyre. S.H. × 1400.

Fig. 50. Capitular membrane and wide first gyre of parabasal body. C.R. × 1765.

Fig. 51. Small specimen. Distribution of peripheral rodlets over capitulum and in most of posterior part of body; adherent spirochaetes. S.H. × 1400.



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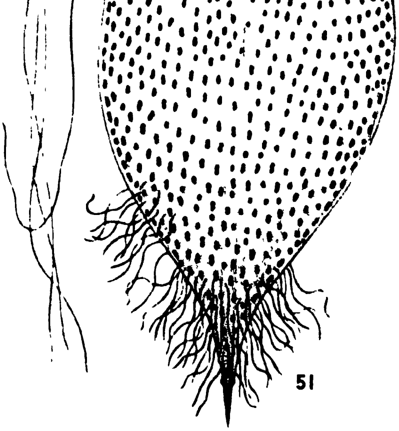

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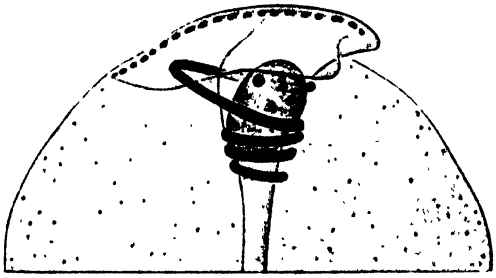

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## PLATE 55

*Hyperdevescovina insignita* sp. nov. from *Neotermes militaris*

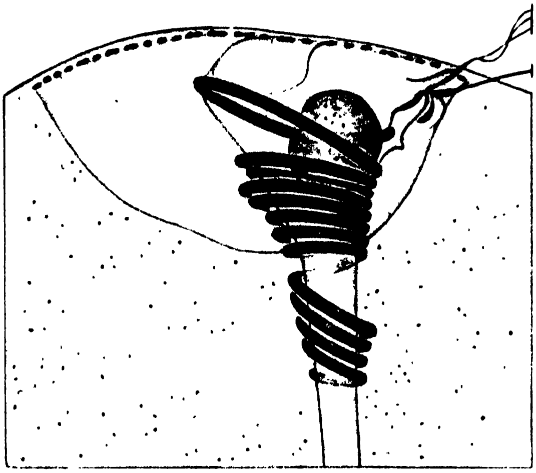
Fig. 52. Relation of parabasal body to capitulum and trunk of axostyle, observed from left side. C.R. × 1765.

Fig. 53. Specimen as seen from right side. Membranous expansion of capitulum here lies over parabasal body. Greater width and separateness of first gyre of parabasal body are characteristic of this species. C.R. × 1765.

Fig. 54. Diagram of capitular rodlets.

Fig. 55. Same specimen as in fig. 51. Internal structures. S.H. ×1400.

Fig. 56. Double individual in which one mastigont is being extruded. S.H. × 1400.



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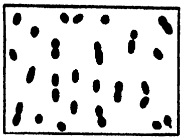

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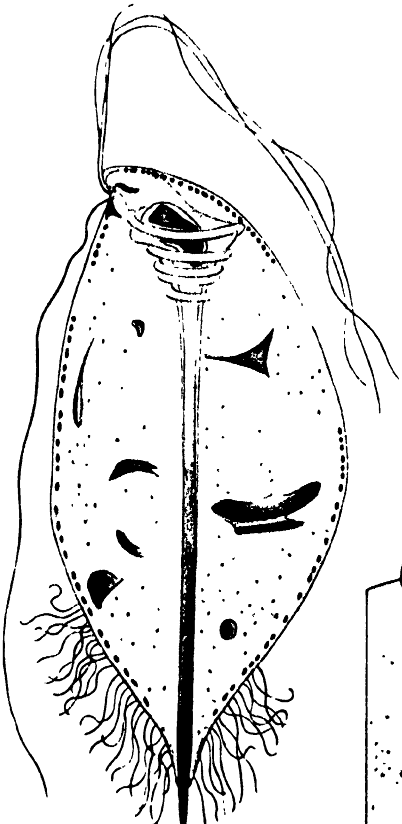

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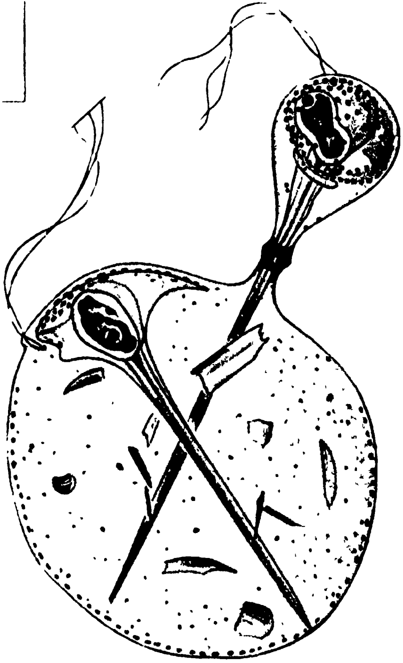

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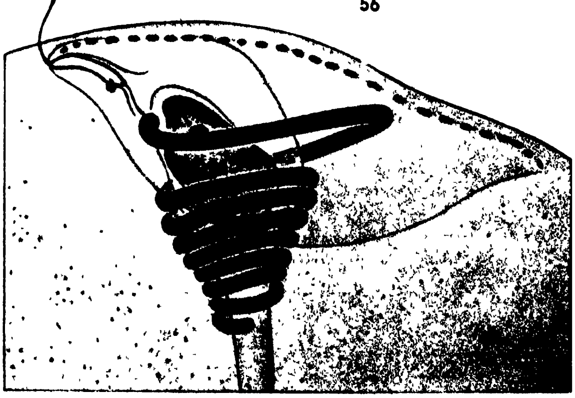

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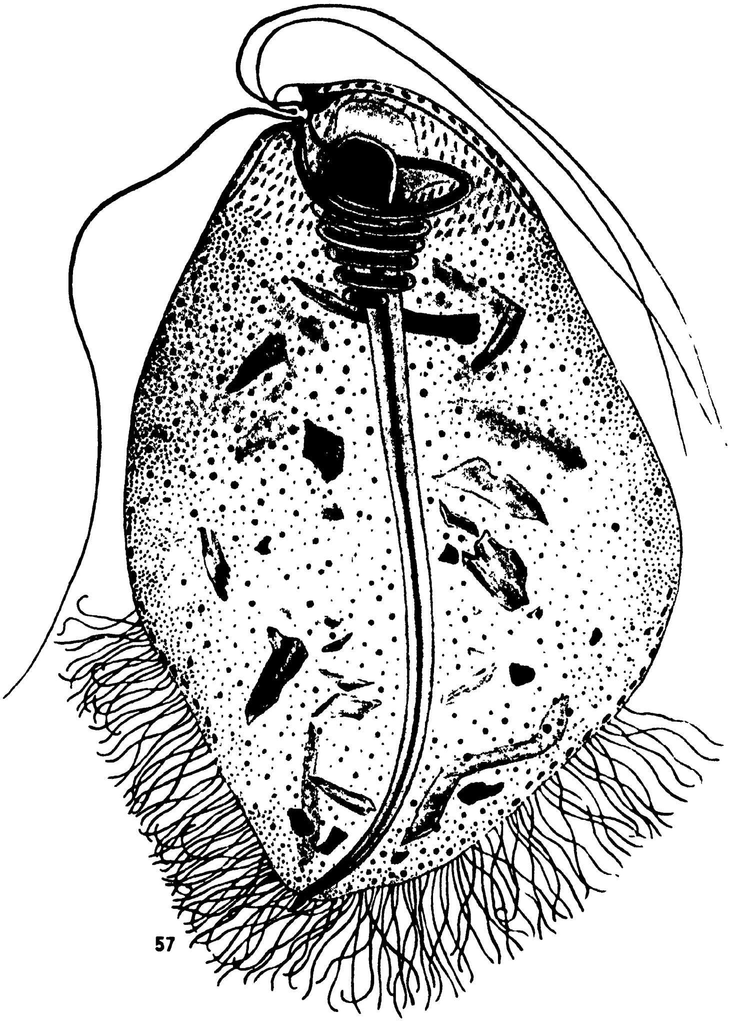
# PLATE 56

*Hyperdevescovina balteata* sp. nov. from *Proglyptotermes spoliator*

Fig. 57. Membranous expansion of capitulum, with overlying rods, at a focus below nucleus; part above nucleus omitted. Nuclear rhizoplast present. Spirochaetes adherent to region of body at posterior end; no anterior spirochaetes. S.H. × 1900.

Fig. 58. Posterior part of axostyle with spikelike end, characteristic taper to this end, and structure shaped like a napkin ring, surrounding spike in its first part. S.H. × 2600.



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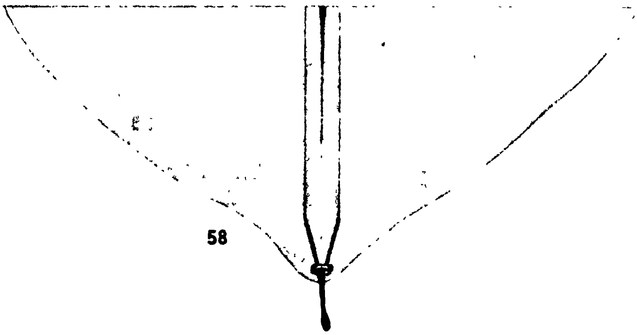

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## PLATE 57

### Figs. 59–62. *Hyperdevescovina balteata* sp. nov. from *Proglyptotermes spoliator*

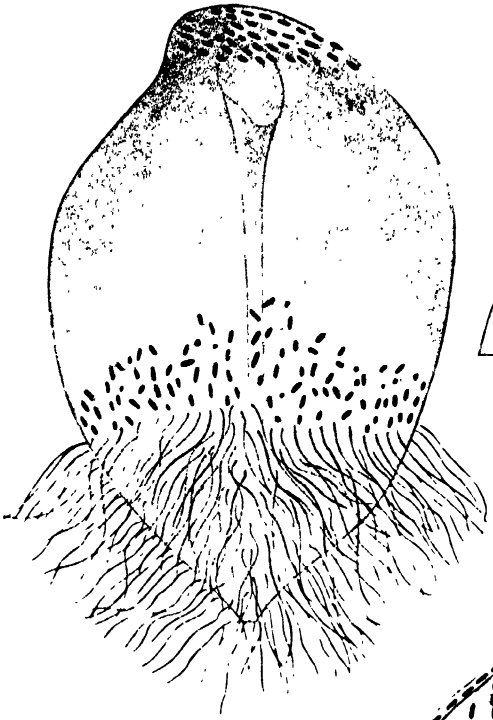
Fig. 59. Distribution of rods over membranous extension of capitulum and in belt around body, with adherent spirochaetes. S.H. × 1535.

Fig. 60. Rods over capitular membrane, aligned in rows; rod-free region around place of origin of flagella. S.H. × 1465.

Fig. 61. Membrane, opposite aspect from fig. 60; irregular alignment of rods. S.H. × 1535.

Fig. 62. Capitular membrane broader in form, so that rods are more spaced out. S.H. × 1535.

Fig. 63. *Hyperdevescovina falcifera* sp. nov. from *Proglyptotermes rufinotum.* Group of rods marking membrane of capitulum is falciform in shape, in contrast to broad, capelike shape in *H. balteata.* S.H. × 1535.



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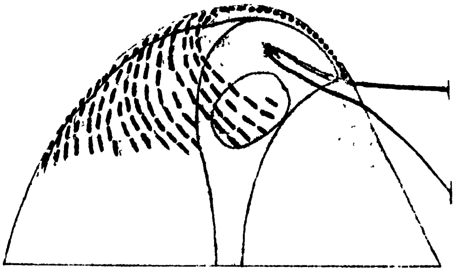

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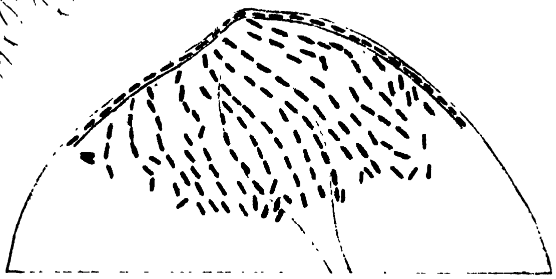

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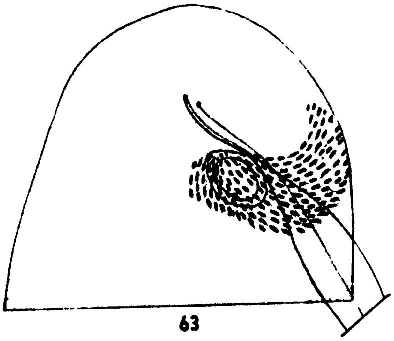

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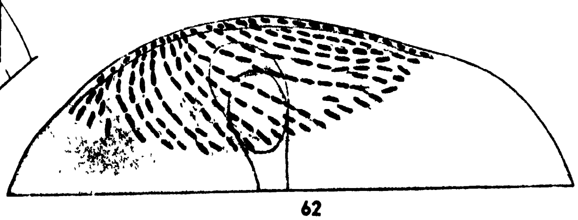

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## PLATE 58

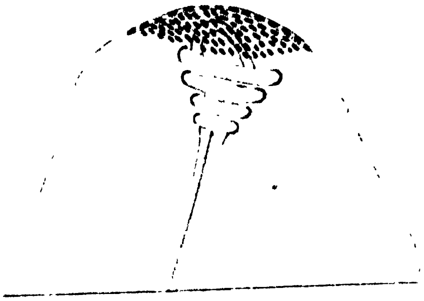
*Hyperdevescovina falcifera* sp. nov. from *Proglyptotermes rufinotum*

Figs. 64–65. Distribution of rods over capitular membrane. Fig. 64 shows lateral aspect; fig. 65, apical aspect. S.H. × 1535.

Fig. 66. Double individual with two mastigont systems, each with falciform capitular membrane. Single belt of rods and group of adherent spiral microorganisms posterior to belt. S.H. × 1700.

Fig. 67. Detail of mastigont structure: cresta; origin of flagella; capitulum and capitular membrane, with overlying rods; parabasal body; trunk of axostyle, with inner membrane. S.H. × 2335.

Fig. 68. Broad side of capitular membrane; detail in shape and distribution of rods. S.H. × 2335.



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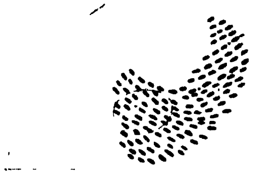

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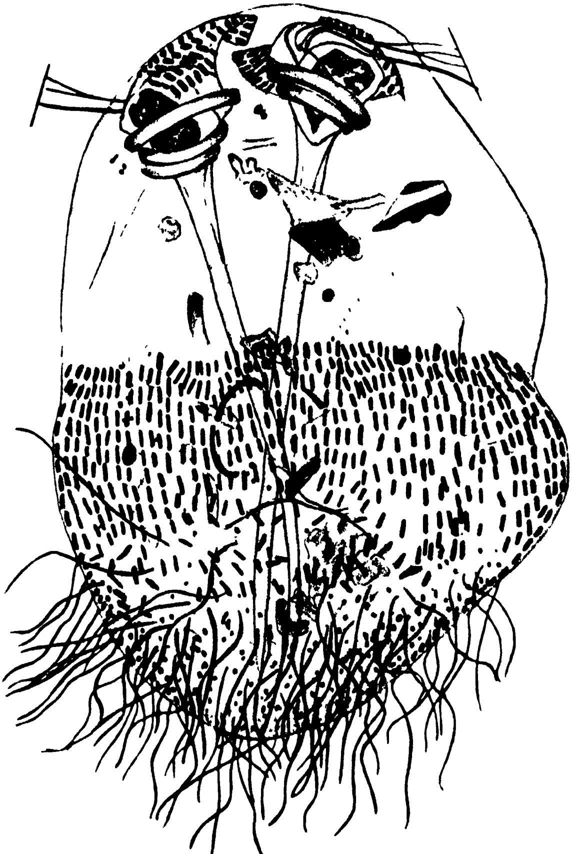

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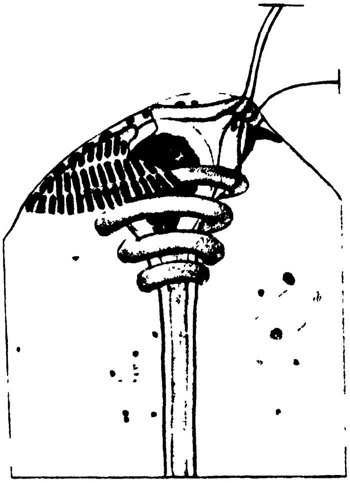

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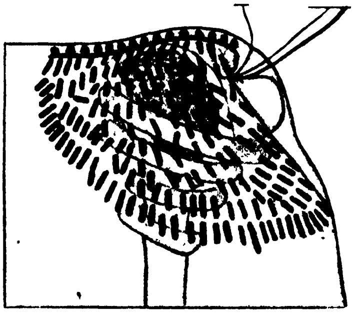

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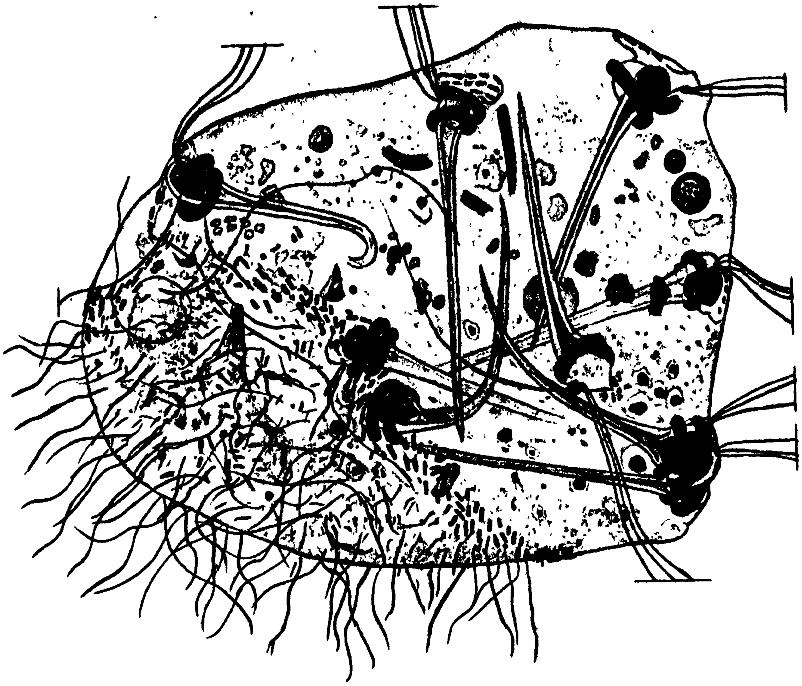
## PLATE 59

Fig. 69. *Hyperdevescovina falcifera* sp. nov. from *Proglyptotermes banksiae.* Nine completely reorganized mastigonts in a common cytosome. One belt of rods and one area to which spiral microörganisms adhere. S.D. × 1150.

### Figs. 70–71. *Hyperdevescovina torquata* sp. nov. from *Proglyptotermes hilli*

Fig. 70. Membranous expansion of capitulum; close, regularly wound parabasal body; cresta; plexus at origin of mastigont structures; parabasal filament at inner edge of helix. S.H. × 2335.

Fig. 71. Nuclear rhizoplast and elongate stainable body near origin of rhizoplast. First part of parabasal is turned anteriorly at angle to helix; vacuoles present in its substance. S.D. × 2335.



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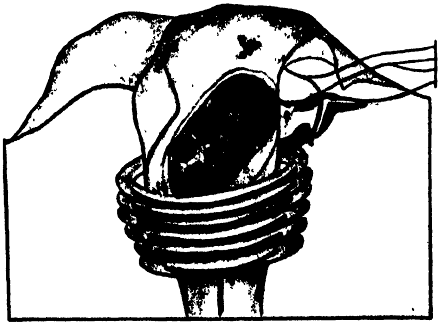

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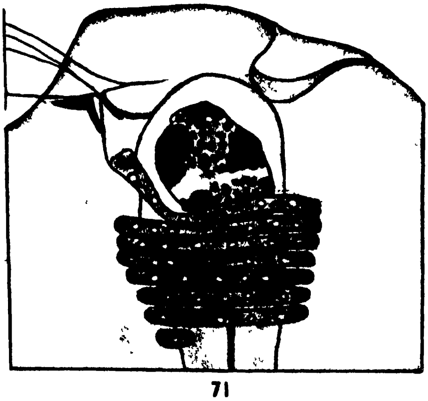

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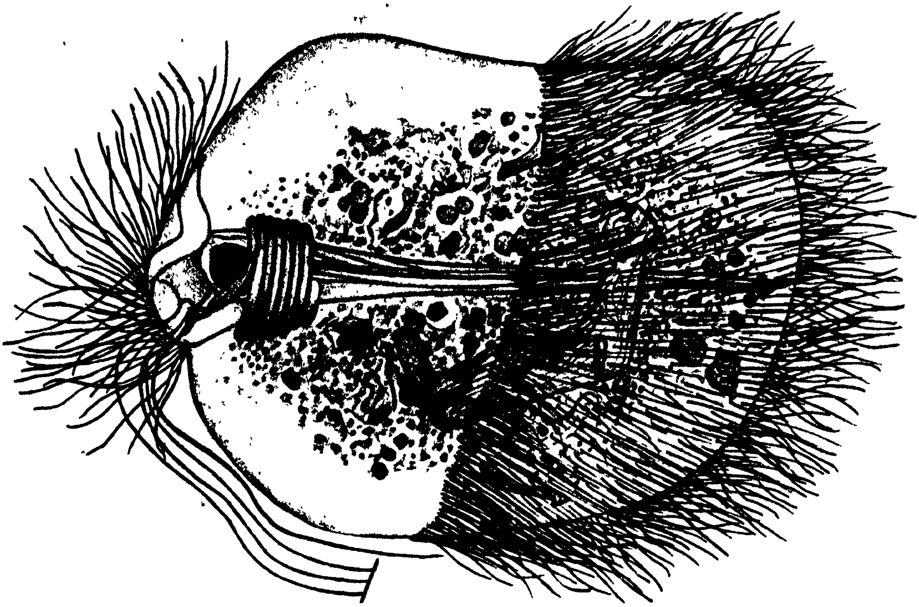
## PLATE 60

*Hyperdevescovina torquata* sp. nov. from *Proglyptotermes hilli*

Fig. 72. Entire specimen, but anterior flagella not shown full length. Regular, broad, closely wound parabasal body is characteristic. Spirochaetes cover posterior half of body and adhere over capitular extension. S.H. × 1200.

Fig. 73. Double flagellate with two mastigont systems, each having group of spirochaetes. S.H. × 1030.



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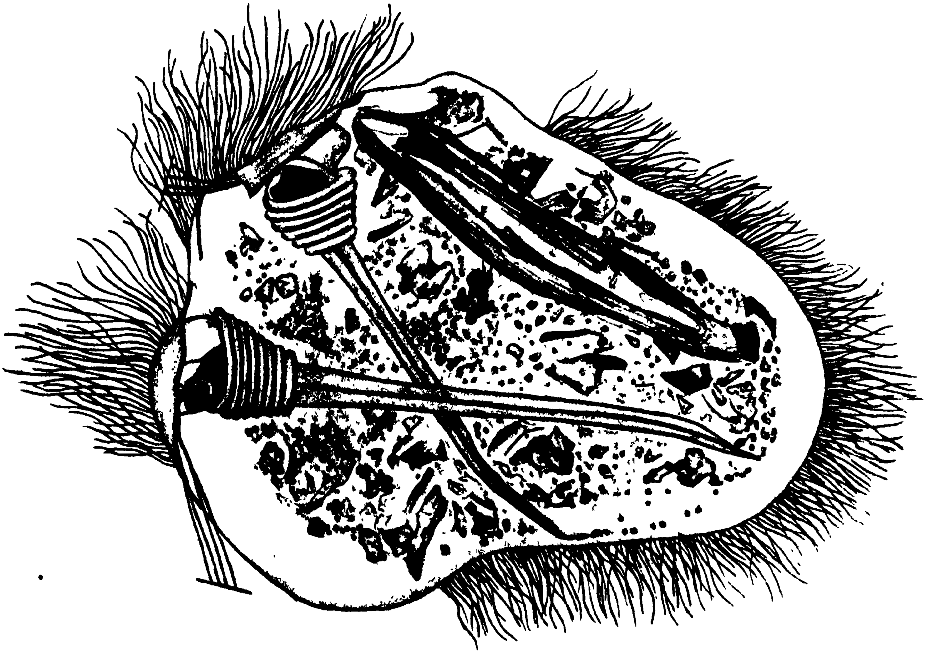

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## PLATE 61

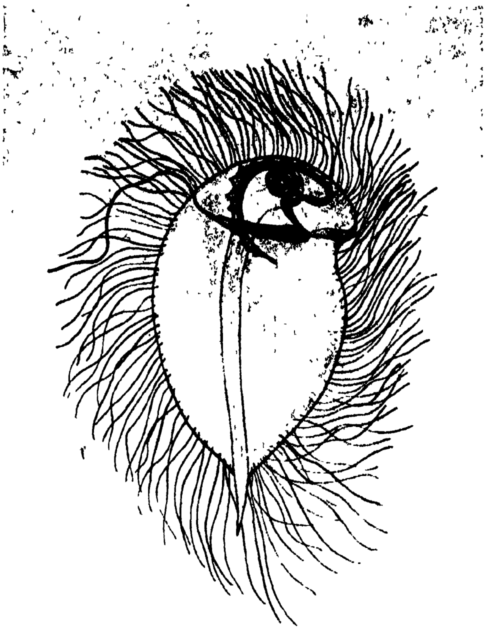
Figs. 74–78. *Foaina serrata* sp. nov. from *Neotermes* sp. nov.
El Salvador

Fig. 74. Entire specimen, but free parts of anterior flagella not shown. Deep-staining serrate band curved through anterior part of body. Covering of spirochaetes. B.H. × 880.

Fig. 75. Larger drawing. Serrate band; cresta; nucleus; trailing flagellum. B.H. × 1800.

Figs. 76–78. Form and position of parabasal body. Nucleus in outline, with nucleolus. Position of blepharoplast represented by small circle at lower end of straight part of parabasal body that is close to dorsal surface of nucleus. From this region, parabasal passes transversely, then anteriorly and dorsally, and finally turns sharply along anterior margin of body. Close to anterior angle is rounded body that stains in same manner as parabasal substance. B.Ehr. × 2140.

Figs. 79–80. *Foaina inflata* sp. nov. from *Neotermes* sp. nov., El Salvador. Large cresta and trailing flagellum, anterior flagella omitted. Parabasal body appears as faintly stained mass beside and posterior to nucleus. Deeply stained filaments along parabasal body and its ramus. B.H. × 1750.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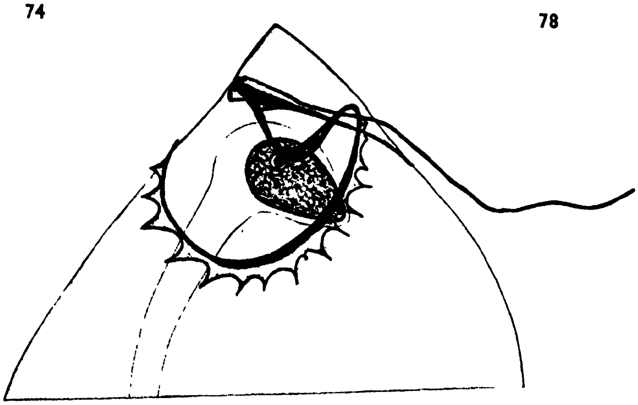
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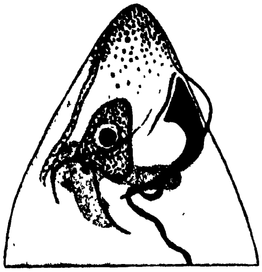
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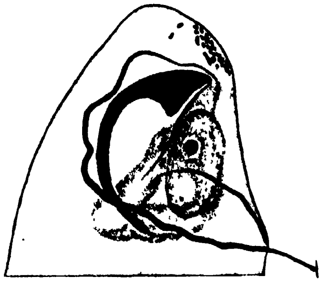
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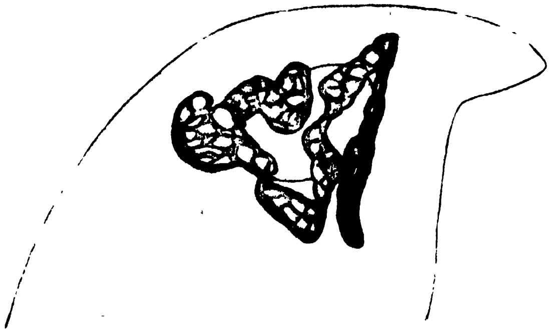
# PLATE 62

*Foaina inflata* sp. nov. from *Neotermes* sp. nov. El Salvador

**Inflated forms of parabasal body, characteristic of that structure in the species. × 1800.**

**Fig. 81.** Parabasal body stained by alum-haematoxylin. Blepharoplast near sharp anterior angle. From this point, parabasal has two limbs in a **V**-form; one is continued transversely with some irregularity and branching. Parabasal substance uneven in outline and vacuolated. B.Ehr.

**Figs. 82–85.** Vacuolization more marked in silver-impregnated specimens, where walls between vesicles are black and interior of vesicles is clear. Basic form is same in all the parabasals—fundamental **V**-shape with one limb extended transversely and sometimes branched. In fig. 82 both limbs of parabasal are inflated. In fig. 84 one is not. In fig. 83 there is branching. In fig. 85 inflation of longer limb is extreme. Cresta is shown in these figures.



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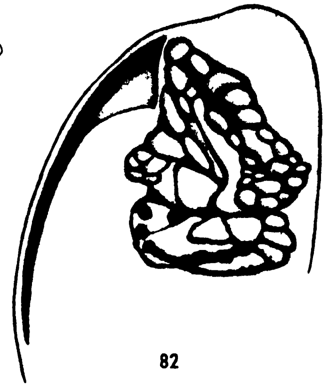

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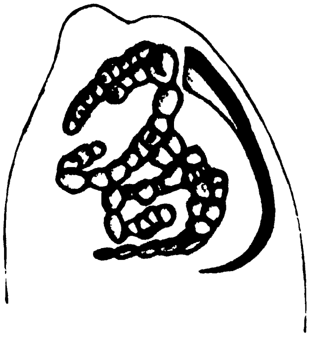

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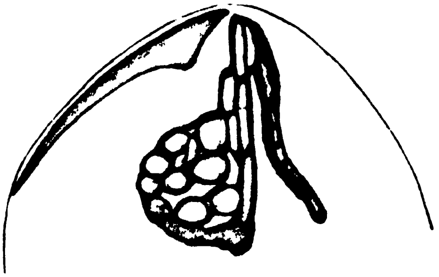

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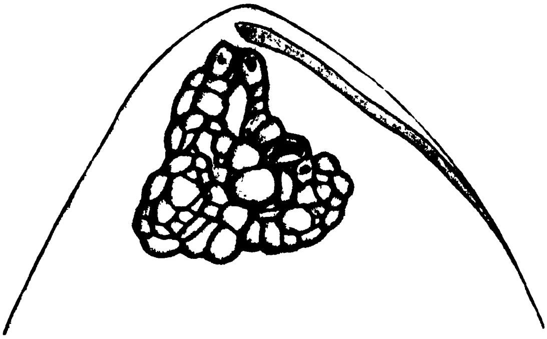

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